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AN ATTEMPT TO CORRELATE THE MARINE WITH THE NON-MARINE FORMATIONS OF THE MIDDLE WEST.

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It is the purpose of this paper to call attention to and to direct investigation along certain lines by which, as it appears to the present writer, we may be able eventually to reach a better understanding regarding the relative age of the various Jurassic and Cretaceous horizons of the Middle West.

It has doubtless frequently occurred to every geologist and paleontologist who has conducted investigations relating to the formations referred to in the title of this paper that marine, terrestrial, fresh and brackish water conditions must have prevailed simultaneously and continuously over extensive areas in our Middle West throughout that long period in middle and late Mesozoic times during which sea and land alternately held dominion over considerable portions of that region. Nevertheless, no serious attempt has been made to correlate the various marine and non-marine deposits with one another. In our geological text-books and in numerous monographs, memoirs and less pretentious papers relating to the geology and paleontology of this region these various formations are described in the text and represented in the accompanying geological columns as occurring in regular sequence one above the other, and the impression is given that where a marine formation is superimposed by a non-marine or *vice versa* the over-

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lying bed belongs to a separate and distinctly more recent age than the underlying deposit. To the present writer this assumption appears in not a few instances to be quite unwarranted, the burden of evidence when carefully considered being in favor rather of considering the two formations, largely at least, as contemporaneous in origin, marine and non-marine conditions having existed simultaneously not over the same but over adjacent regions, each giving origin to its characteristic deposit and the marine beds appearing above or below the non-marine according to whether the sea was encroaching upon or receding from the land-mass during the period of their deposition.

The physical conditions that prevailed during the deposition of any geological formation or series of formations and the manner in which a marine deposit is replaced by a non-marine or *vice versa*, are best understood by a study of those regions where, under existing conditions, similar deposits are in process of formation. As an illustration let us consider the conditions that at present prevail almost continuously along our Atlantic coast from Florida to Long Island. Throughout this entire coast line a broad and little elevated coastal plain extends inland from the sea to the eastern foothills of the Appalachian Mountains, while to the eastward of this coast line there lies an equally broad and gently inclined continental plateau at present but little submerged beneath the sea. The eastern limit of this submerged portion of the continental plateau may be regarded as having formed the coast line of the continent at some former period in our earth's history, when the eastern portion of this continent stood at a greater elevation than at present. It was during this earlier period of increased elevation that the Appalachians suffered most from denudation and that the coastal plan, together with the submerged continental plateau, were formed, not as at present differentiated, but as a continuous coastal plain reduced by erosion to a more or less uniform base level extending westward from the eastern limits of the present continental plateau to the foothills of the mountains. A glance at any good map of this region will reveal the fact that the entire coast line, more especially to the northward of Charleston, is deeply indented by numerous shallow sounds and bays, like Delaware and Chesapeake Bays in the north and Albemarle and Pamlico Sounds farther south, while the country for many miles inland from the coast frequently consists largely of more or less impenetrable

marshes, such as the Dismal Swamp in Virginia and North Carolina and others bordering the lower courses of the James, Roanoke, Cape Fear, Pedee, Neuse and Savannah rivers, and to a less extent the Potomac, Susquehanna and Delaware rivers farther north.

If we trace the courses of the larger rivers of this region, those rising in the Appalachians, from their sources to their mouths, the course of each will be found to be divisible into three sections, when considered according to the eroding and transporting power of the stream. The first of these three sections, commencing above, extends from the source of the stream to the point where it leaves the foothills of the mountains and emerges upon the coastal plain. Throughout this portion of its course the stream is both an eroding and a transporting agent, displaying about equal efficiency in either capacity. Below this point, which has been called the "Piedmont escarpment," the stream ceases to be to any great extent an eroding agent, and between the foothills and the swampy region bordering the coast it is chiefly a transporting agent, the current being too sluggish to accomplish any appreciable amount of erosion, and at times becoming so slow as to permit of considerable deposition. Between that point where it enters the marsh lands and its mouth the stream drops all that remains of its load of sediment, save that which is carried seaward by the action of the tides, aided to some slight extent perhaps by the feeble current of the stream, which has now become almost entirely an agent of deposition.

Now if we turn our attention to the changes that are taking place in the region traversed by these rivers, it will be seen that the first section, or that between their sources and the Piedmont escarpment, is one almost exclusively of degradation, there being little or no deposition going on in this region, while throughout the second section, that lying between the escarpment and the swamps along the coast, the eroding and depositing agencies are unimportant, though about equally effective, resulting on the whole in comparatively little change in the topography, while in the third region, or that lying between the swamps and the coast, deposition is taking place with considerable rapidity. The inland swamps are being filled in, while along the coast of Virginia and North Carolina the estuaries and sounds located at the mouths of the various rivers or enclosed between the mainland and the low sand spits, thrown up by the waves and extending almost continuously along the coast,

are receiving vast quantities of material from the numerous streams emptying into them and are destined at some future time to be converted into fresh-water swamps like those now found inland, while the coast will be pushed farther eastward, repeating the same or very similar conditions.

If now we examine the material that is being deposited at various localities, commencing with that point on the coastal plain where deposition is more rapid than erosion, and extending eastward not only to the coast line but beyond to the eastern border of the continental plateau, we shall find that deposits of every character, from fresh water to estuary or brackish, littoral and purely marine, are being formed simultaneously, in each of which are preserved remains of the life characteristic of the conditions attending its deposition. In the swamps will be found peat bogs and beds of sand, clay and marl, with remains of terrestrial and fresh water vertebrates and invertebrates. Over the river bottoms will be found fluviatile deposits. In the estuaries, bays and sounds beds with the remains of a brackish water fauna are forming. Outside the sand spits that enclose Albemarle and Pamlico Sounds will be found other beds of sand with a littoral fauna. Still farther seaward and continuing to the limits of the submerged continental plateau a typically marine deposit is being laid down with remains of its characteristic fauna. Beyond this we reach the abysmal depths of the ocean with a fauna and deposit distinct from any of the others mentioned. Assuming that the average depth of the ocean just west of the eastern border of the continental plateau is 3000 feet, and that the western limit of true marine conditions extends to within fifty miles of the eastern limit of true fresh water or terrestrial conditions, we have then within a distance of fifty miles from east to west every character of deposit from terrestrial and fresh water to true marine forming at the same time; and if we continue our section to the eastern limit of the continental plateau, at altitudes differing more than 3000 feet from one another, as indicated by the curved line *a*. *a'*. which in the accompanying diagram, seen in figure 1, represents an imaginary line drawn along the surface of the ground and bottom of the sea from the western border of the swamps lying west of Pamlico Sound in North Carolina, across this sound and eastward to the eastern border of the continental plateau. Along this line *a*. to *b*. is the swamp region with fresh water deposits, *b*. to *c*. Pamlico Sound with its estuary depos-

its, *c.* to *d.* the shallow water and littoral deposits extending eastward from the coast, *d.* to *a.'* true marine conditions.

Let us suppose present conditions to continue without any elevation or depression of the earth's surface in this region, until by the process of erosion and deposition the present coast line is advanced to a position approximating that of the eastern limits of the continental plateau, as shown in the curved line *a.'–a."* We would then have deposited between the lines *a.–a.'* and *a.'–a."* sediments aggregating in vertical thickness something more than 3000 feet, and comprising four formations more or less distinct when considered from their faunal and lithological characters but of the same age, all four having been laid down in the same time interval and all conformable with one another save for an unconformity by

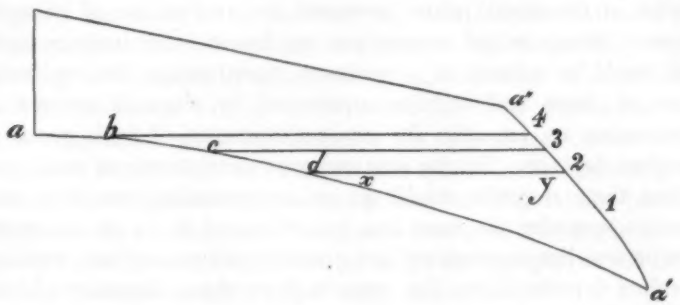


Fig. 1.

overlap along their western borders necessitated by the topography existing at the time when present conditions were inaugurated. Commencing below, No 1. of these four formations would be the thickest of the series and would form a wedge of purely marine and deep water deposits at the base with the blade directed westward. Above these deep water deposits would come No. 2 of the series, a marine shallow water and littoral deposit of nearly uniform thickness, which would be determined by the depth of water at which such deposits may take place. This would contain a littoral fauna and would overlap the western border of No. 1. Above this and overlapping it on the west would come No. 3, an estuary formation with its beds of oysters and other brackish water mollusca, now occurring in such abundance in the sounds and bays of this coast. The vertical range of these brackish water deposits, like that of No.

2, would, of course, be limited if, as we assumed above, perfectly stable conditions of the earth's surface were maintained in this region during the entire period required for the eastward extension of the coast line from its present position to that of the eastern border of the submerged continental plateau. Above No. 3 would come No. 4, the uppermost of the series, a fresh water and to some extent aeolian deposit, with its beds of peat transformed perhaps into lignite and remains of a terrestrial and fresh water vertebrate and invertebrate fauna. The thickness of these fresh water deposits would not be limited as would that of Nos. 2 and 3 of the series, since as the coast line advanced eastward it would leave behind a low and flat region growing continually wider from east to west and increasing very slowly in elevation by the accumulation over its surface of fluvial, lacustrine and aeolian deposits. As the width of the coastal plain increased the inclination of its surface toward the sea would become less and less and the drainage or run-off would be reduced to a minimum, transforming the region into one of lakes and marshes connected by sluggish streams and increasing its capacity for the accumulation of fresh water and aeolian deposits. By the uninterrupted continuance of such conditions these deposits would go on accumulating over this entire region long after the shore line had advanced far to the eastward of its present limits, resulting in a greater thickness of fresh water and aeolian deposits along the western than along the eastern border. These deposits would therefore form an overlying wedge with the blade directed eastward, or in a direction opposite to that of the wedge of marine deposits constituting No. 1 at the base of the series, and tending to produce a somewhat uniform thickness of the combined series of beds, with the fresh water deposits predominating in the western region and the true marine deposits in the eastern, while the interstratified brackish water and littoral deposits would continue practically of the same uniform thickness from the eastern to the western border of the region.

Thus far we have only considered what would take place here under perfectly stable conditions in the earth's crust. Let us next consider what would result from certain oscillations in the earth's surface along this coast.

If a period of elevation should set in affecting the coastal plain and submerged continental plateau the effect would be to hasten the recovery of the continental plateau from the sea and to decrease

the thickness of the various deposits forming in this region. Moreover, if the elevation to the westward should become appreciably more rapid than to the east the run-off would be increased by the greater inclination of the surface toward the sea, and a period of erosion would be inaugurated over a considerable portion of that area where formerly fresh water deposits were being formed.

If on the other hand the region should undergo a general but gradual subsidence, so gradual that the rate of upbuilding by deposition would be more than sufficient to keep pace with the subsidence, the result would be a lengthening of the time necessary for the coast line to advance eastward from its present position to that of the eastern border of the continental plateau and a corresponding increase in the thickness of the various deposits. Under such conditions the thickness of the littoral and estuarine or brackish water deposits would not be so restricted as under those conditions previously considered, but these might attain to almost any depth, varying in thickness at any given point according to whether the rate of subsidence during the deposition of these deposits at such point approximated or fell far below the rate of sedimentation taking place there. The more nearly the rate of subsidence approximated that of sedimentation at any point where littoral and brackish water conditions prevailed, the greater would be the length of time necessary to recover the area from the sea and the greater the thickness of the littoral and brackish water deposits.

If at any time the rate of subsidence exceeded that of sedimentation, conditions would immediately be reversed, the sea would encroach upon the land, the coast line would recede to the westward, and the fresh water beds seen at No. 4 in the diagram would be overlaid first by a brackish water deposit, over which would be laid down a littoral deposit, followed later by beds of deep water origin as the subsidence increased and the sea advanced upon the land. If this period of more rapid subsidence were only temporary it would result merely in a local interstratification of fresh water, brackish and marine deposits. If on the other hand it became permanent it would result in the entire resubmergence of the region already recovered from the sea, and there would be a repetition in reversed order of the fresh water, brackish, littoral and true marine deposits already described as having been formed during that period when the land was advancing upon the sea. At the close of his period of subsidence, when the sea had regained its original

shore line, a section through the deposits formed before and during this period would exhibit a structure similar to that shown in the second diagram, where *A.* represents a wedge of fresh water deposits immediately overlaid and underlaid by the brackish water beds *B. B.*, followed above and below by the littoral deposits *C. C.*, which are in turn underlaid and overlaid by the true deep water marine beds *D. D.*, and the time interval during which the single fresh water formation represented by *A.* was deposited will have equaled that employed in the deposition of the underlying and

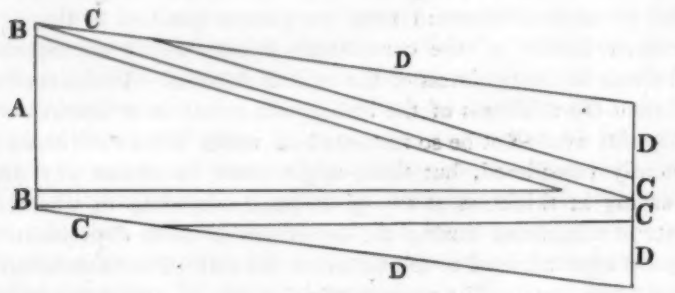


Fig. 2.

overlying marine and brackish water beds combined. The fresh water beds should, therefore, be correlated with both the underlying and overlying marine beds.

The actual conditions at present existing along our Atlantic coast, together with the possible results following a long continuance of these conditions, with variations similar to those outlined above, have evidently been repeated at certain intervals in Mesozoic times throughout our Middle West.

The Judith river beds at about the middle of the Upper Cretaceous, together with the overlying and underlying marine formations, known respectively as the Pierre or Bearpaw shales and the Claggett formation, form a splendid example of the conditions illustrated in the second diagram. They are composed of a series of deposits for the most part of fresh water origin, but overlaid and underlaid by brackish water beds. They attain to a known thickness of something over 500 feet and extend continuously from the Saskatchewan river region in Canada to southern Montana. They are well developed along about the 110th meridian of west longitude, where they may perhaps be regarded as attaining their maxi-

mum thickness. Some distance to the eastward of this meridian, however, they decrease in thickness and finally disappear, passing into the overlying and underlying marine beds mentioned above. In the second diagram *A*. would represent the fresh water and middle portion of the Judith river beds, *B*. *B*. the underlying and overlying brackish water beds usually referred also to the Judith river formation, while *C*. *C*. and *D*. *D*. inclusive would represent the Bearpaw shales at the top and the Claggett formation at the bottom, *C*. *C*. representing littoral deposits or passage beds from brackish water to true marine deposits and occurring everywhere throughout this region both at the top and bottom of the Judith river beds.

Having now seen how two or more formations occurring in regular sequence one above the other may originate simultaneously instead of pertaining to different and distinct ages, let us next consider what bearing this will have on the relative age of different horizons in any one of these formations. To the paleontologist this is an important point, since in working out the phylogeny and relations of fossil forms within the same formation it is often of the greatest importance to know whether a given genus or species preceded or succeeded another, or if the two were contemporaneous. Heretofore we have been inclined to consider any given stratum within a formation as having been deposited near the beginning, at about the middle or near the close of that time interval during which the formation was laid down, according to whether it occurs near the top, in the middle or near the bottom of the formation and regardless of the geographical position of that point at which the stratigraphical determination was made. To say that two fossils were found fifty feet beneath the top of a given formation which had not been subjected to erosion, but at a distance from each other of several, perhaps many miles, has usually been regarded as establishing for them an identical or very similar age. Every consideration has been given to the stratigraphic position, none to the geographic. Yet in not a few instances the latter is of equal or even far greater importance than the former, and must be considered in determining at just what period in the time interval necessary for the deposition of a certain formation any given stratum was laid down. Furthermore, we have been accustomed to estimate the time employed in the deposition of any given formation solely by its vertical thickness, and regardless of its geographical

extent assuming that conditions were more or less uniform over the entire region occupied by the formation from the beginning to the close of its deposition—an assumption wholly unwarranted, as we have seen in formations deposited under conditions similar to those represented in the first diagram and more especially in the littoral and brackish water beds, represented respectively by 2 and 3. In beds such as these the actual area over which deposition takes place at any given time is limited to a narrow strip along the coast, and materials are there being added simultaneously and continuously throughout the entire vertical extent of both these beds. It is thus evident that in deposits such as these geographical distribution rather than vertical thickness is the basis upon which to estimate the length of time employed in their deposition. The age of any fossil found in these beds will be greater or less than that of another found at a different locality, not according as to whether it occurred at a higher or lower level in the series, but according to the difference in the geographical position of each relative to the original coast line, and the actual difference in age will, of course, depend upon the difference in the geographical positions at which the two occurred and the rate of advance or recession of the coast. The difference in age would be expressed in years by dividing the distance between the two localities, measured along a line at right angles to the original coast line, by the annual rate of advance or recession of the coast.

Let us consider again the conditions at present existing along our Atlantic coast and represented in the first diagram. It will be readily apparent that as the coast line is advanced eastward by the deposition of the material brought down by the streams, the western limits of true marine, littoral and brackish water conditions will be more and more restricted and that marine conditions with a depth of sea of more than 2000 feet will prevail over the region near the eastern border of the submerged continental plateau long after the present coast line has advanced to the position shown at *X.* on the diagram, while to the westward of this position the region has all been brought above sea level and only fresh water and aeolian deposits are being formed. It is evident then that when the coast line has been advanced to *a.''* the uppermost stratum of the marine formation, No. 1, will not be of uniform age from *X.* to *Y.*, but that this stratum at *X.* will exceed in age the same stratum at *Y.* by the length of the time required for the

coast to advance from *X.* to *Y.*, represented at *Y.* by a vertical thickness of deposits of about 2000 feet.

With the overlying brackish water and littoral formations represented by Nos. 2 and 3, the stratigraphic position of any horizon at any locality within either would be of minor importance in determining its age relative to the formation as a whole. Since the deposition of these beds would not take place simultaneously over the entire area of their distribution, but would be restricted to a narrow belt along the coast which would move eastward as the coast advanced, it is evident that these deposits would be oldest to the west and newest toward the east. This is an instance where geographical position is of far more importance than stratigraphical in determining the relative age of a given stratum within a formation.

From the above observations it appears to the present writer that other elements than their present stratigraphic position relative to one another must be considered in determining the age and in correlating any series of formations deposited along a receding or advancing coast. There is evidence that several of the Mesozoic formations of our Middle West were deposited under such conditions. It should first be determined whether the sea was advancing or receding during the deposition of any given series. Next the direction taken by such advance or recession of the sea should be ascertained, in order to determine in what geographical position the older beds of the series are to be found. Then the rate of deposition as compared with the rate of advance or recession of the sea should be determined, so as to be able to correlate with one another, approximately at least, strata within the same formation but occupying different geographic and stratigraphic positions. In the following attempt to correlate various formations in the region referred to the methods and principles outlined above have been applied only in a very general way, and the results can only be considered as suggestive of what might be accomplished by more extended observations and careful determinations in the same region.

The Atlantosaurus Beds and Dakota Sandstones considered as the possible equivalents of the Upper Jurassic and Lower Cretaceous.

There is a considerable thickness of non-marine sandstones and shales with a wide geographical distribution in the region under question, concerning the age of certain members of which there has been much difference of opinion. The lower member of these was

first differentiated by Marsh who named them the *Atlantosaurus beds*.[1] They have since received various other names by other authors, such as the Como beds, the Morrison beds, the Beulah shales, etc. Since these later names are no more appropriate than the one first given there is no good reason for accepting any of them and rejecting the name first bestowed on these beds by their discoverer. Moreover, if stability in geological nomenclature be desirable there would seem to be no better way of securing it than by recognizing priority. It may be well to adopt certain rules governing the formation of new names for new formations, but these rules should not be made retroactive in their application, since such application will not only fail to do full justice to many earlier geologists but, what is of far more importance, will result in increasing still further that synonymy already existing in our geological nomenclature.

In their typical exposures the Atlantosaurus beds consist of rather fine shales. At certain localities there are in them occasional small lenses of limestone with fresh water invertebrates and more important lenses of sandstones frequently appearing as distinct and quite continuous strata. Toward the top the sandstones become more frequent and the whole is everywhere overlaid by a heavy bed of sandstone known as the Dakota sandstones, save where these have been removed by erosion. In some places the passage from the sandstones and shales of the Atlantosaurus beds to the Dakota is quite abrupt, but as a rule it is very gradual, the two grading into one another in such manner that it is difficult to say where the one ends and the other begins. Both these formations are of fresh water and aeolian origin, though there is evidence of brackish water or littoral deposits in a few places near the top of the Dakota.

The Dakota sandstones have usually by general consent been considered as representing the base of the Upper Cretaceous, both from their stratigraphic position beneath the Benton and from their fossil flora. The latter, however, can scarcely be considered as being at present at least of any special value in determining the exact age of these sandstones, which in many places in the western portion of the region under consideration pass insensibly below into the sandstones and shales of the Atlantosaurus beds. In the region near Buffalo Gap, S. D., Darton has distinguished these transitional

[1] The *Hallopus beds* of the same author are disregarded here as of minor importance and being usually not distinguishable.

beds as the Lakota formation and has discovered in them dinosaurian remains representing types differing from and distinctly more recent than those commonly met with in the typical Atlantosaurus beds. Moreover at several localities these transitional beds have yielded cycads and other plant remains which, according to Prof. L. F. Ward who has studied this flora, are of Lower Cretaceous types. At present the dinosaurian fauna is too meagre to determine certainly whether its affinities are with the Jurassic or Lower Cretaceous. Its aspect is however, in so far as we know it, more modern than that of the typical Jurassic. The Predentata appear to be assuming the predominant position held throughout the Jurassic by the Sauropoda, and I am inclined to consider the dinosaurian fauna as indicative also of a Lower Cretaceous age for these beds.

The Atlantosaurus beds, consisting of dark shales with intercalated sandstones, have a wide distribution throughout the western portion of the region under consideration, where they appear at the proper position in the geological section encircling every mountain upthrust and occupying many of the intermediate valleys. These beds contain the remains of an exceedingly rich and varied dinosaurian fauna, concerning the age of which there has been some difference of opinion. At present, however, this fauna together with the beds containing it is very generally regarded as of Jurassic age. There are, however, certain geologists and paleontologists who still regard these deposits as of Lower Cretaceous age. The dinosaurs, which probably offer the most reliable evidences as to the age of these beds, are unmistakably Jurassic in type, whether the comparison be made between the individual species or the faunas as a whole. Marsh was wont to correlate the Atlantosaurus beds with the Wealden which he regarded as of Upper Jurassic age, but which is now usually placed at the base of the Lower Cretaceous. It is not quite clear upon what evidence Marsh relied when making this correlation. The dinosaurian fauna of the Wealden is certainly quite different and more modern than that of the Atlantosaurus beds. In the Wealden the Sauropod dinosaurs, which form such a conspicuous feature in the faunas of the Middle and Upper Jura, are on the wane and that group of Predentate dinosaurs known as the Iguanodontia has attained unusual importance, assuming to a certain extent at least the position formerly held by the Sauropoda. In the Atlantosaurus beds, however, the Sauropoda predominate and

the Iguanodont group of the Predentata are represented by smaller and less specialized forms. The dinosaurian fauna of the Atlantosaurus beds as we now know it is certainly more nearly allied to that of the Kimmeridge and the underlying Oxfordian than to the Wealden or the Purbeck, and there is little doubt that the true Atlantosaurus beds, those lying below the Lakota of Darton, are of Upper Jurassic age.

Throughout the northern area of their distribution the Atlantosaurus beds are conformably underlaid by a series of marine deposits variously known as the Baptanodon beds, the Shirley beds, the Sundance formation, etc., and universally referred to the Upper Jurassic. That these beds are of Upper Jurassic age has not been questioned and is abundantly confirmed by both their invertebrate and vertebrate faunas. About the Black Hills in South Dakota, the Big Horn Mountains in northern Wyoming, and at other places these marine beds attain a considerable thickness, 400 to 500 feet, while the overlying Atlantosaurus beds of fresh water origin show a more restricted development in these regions than they attain farther to the southward. As we proceed southward, however, the marine deposits diminish in thickness and disappear altogether near the boundary line between the States of Colorado and Wyoming. Farther south the Atlantosaurus beds attain to a maximum thickness of perhaps 500 feet and rest directly but unconformably upon the "Red Beds," now usually considered in their upper members at least as of Triassic age, but formerly referred to as the Jura-Trias. Still farther south in New Mexico, Lee has found conditions which lead him to believe that these fresh water beds are continuous with marine beds of Lower Cretaceous age pertaining to the Comanche series. Though the evidence is at present not at all conclusive and nothing is known concerning the character of the vertebrate fauna of the fresh water beds at this locality beyond the fact that they contain dinosaurian remains, yet it is quite possible that the upper members of this series, the Lakota of Darton, may pass eastward into true marine deposits of Lower Cretaceous age.

To the eastward the Dakota sandstones, at the summit of the series of fresh water and aeolian deposits under discussion, overlap the underlying Lakota sandstones and Atlantosaurus beds, and in eastern South Dakota, Nebraska and Kansas they rest unconformably upon strata pertaining to the Carboniferous or Permo-Carboniferous.

From the foregoing remarks it will appear that in the region referred to in the title of this paper there is a conformable series of marine and fresh water or in part aeolian deposits, commencing below in the north with marine beds unquestionably of Jurassic age and passing upward and toward the south and east into a series of fresh water and aeolian deposits containing a dinosaurian fauna, with affinities clearly allying it also with the Upper Jurassic and another still later horizon, the Lakota of Darton, with a Lower Cretaceous flora and a dinosaurian fauna of the character of which as yet little is known, but which is certainly more recent than that of the true Atlantosaurus beds, the entire series terminating above in the Dakota sandstones generally referred to the base of the Upper Cretaceous. This entire series rests unconformably upon the "Red Beds" in such manner as to show conclusively that prior to the beginning of its deposition there was in this region a long and continued period of erosion, embracing perhaps the close of the Triassic and a considerable portion of the Jurassic. At the top the Dakota sandstones are overlaid with apparent conformity by the Benton, the lowermost marine member of the Upper Cretaceous. As yet no evidence has been advanced to show that sedimentation was not continuous in this region from that period which marked the beginning of the deposition of the marine Baptanodon beds at the base of the series to the close of that much later period which witnessed the deposition of the Dakota sandstones, and I see no reason why this series of deposits may not represent in this region the entire Lower Cretaceous and Upper Jurassic, as their floras and faunas and the stratigraphy and conditions of sedimentation would seem to indicate. I am well aware of the enormous time interval which a correlation such as that just suggested presupposes for the deposition of this comparatively meagre series of deposits, aggregating a thickness nowhere of perhaps as much as 1000 feet and in no way comparable with the thousands of feet of beds which in other regions are known to be included in the Lower Cretaceous alone, to say nothing of the Upper Jurassic. Nevertheless this objection does not seem an especially important one when we consider the wide geographical distribution of those non-marine deposits which constitute by far the greater bulk of this series, and the time interval necessary for the deposition of which, as we have seen at the beginning of this paper, should be estimated not so much by their vertical thickness as by the extent of their geographical distribution.

Non-Marine Equivalents of the Marine Beds of the Colorado and Montana Formations.

Between the Dakota sandstones and the base of the Tertiary there is in this region a number of formations the characters of which are indicative of littoral, brackish, fresh water and terrestrial conditions.

The lowermost of these is the Eagle formation, consisting for the most part of massive sandstones with intercalcated beds of lignite and shales. This formation is known to have a considerable distribution in Montana and it doubtless extends northward into Canada. In general it is not very fossilferous, but in places, usually of very limited extent, it has been found to contain in considerable abundance marine invertebrates, indicative of littoral conditions. Although as yet no fresh water vertebrate or invertebrate remains have been found in these beds, yet the nature of the materials composing them and the manner in which the sandstones, shales and lignites replace one another are indicative of an adjacent land mass, and it is quite probable that they are to some extent at least of fresh or brackish water origin. A few remains of terrestrial vertebrates have been found in them. They afforded the type of *Ornithomimus grandis* Marsh and other fragments of terrestrial dinosaurs. The presence of these remains may be considered as additional evidence of an adjacent land-mass.

The Eagle formation is conformably underlaid and overlaid respectively by the Benton and the Claggett formations. Its stratigraphical position is nearly, perhaps identically, the same as that occupied by the Niobrara farther to the southeast, and it was I think quite properly correlated with that horizon by Mr. Earl Douglass, though I should not be in favor of applying the same name, as was done by Mr. Douglass, to formations so different in lithological and faunal characters. From the nature of these deposits it is evident that toward the close of the Benton there was in this region a decided change of conditions which materially altered the character of the sedimentation, and that the true marine conditions which had prevailed continuously throughout the Benton gave place to at least shallow waters and in part perhaps to brackish and terrestrial conditions, though it is evident from the character of the beds composing the Eagle formation that the transformation was by no means so complete at this interval as during the preceding one which witnessed the deposition of the Atlantosaurus beds and

Dakota sandstones, or the two succeeding intervals marked by the deposition of the Judith river beds and the Laramie.

After the deposition of some 300 to 400 feet of the sandstones, shales and lignites of the Eagle formation true marine conditions were again restored in this region. That this return to marine conditions was gradual and due to a slow advance of the sea over the region in question is evidenced in certain places by the manner in which the uppermost Eagle sandstones pass by a series of shales and lignites into the overlying true marine beds of the Claggett formation, and is well shown on Eagle Creek a short distance above where it empties into the Missouri river, some twenty miles above Judith, Mont., at a place which may be regarded as the type locality for the Eagle formation.

Although we have not been able to trace this formation continuously to the east and south and to observe its actual passage in those directions into the overlying and underlying marine formations, yet we do know that it disappears in these directions and is entirely replaced by marine deposits resembling those of the Niobrara and the base of the Montana. From all the evidence at hand it seems probable that over the region now occupied by the Eagle formation shallow water and in part terrestrial conditions prevailed for a considerable period, commencing toward the close of the Colorado and continuing uninterruptedly well up into the Montana, and that this formation should be correlated with the upper portion of the Colorado and the lower portion of the Montana.

After the deposition of the Eagle formation marine conditions again prevailed over this region, as is evidenced by the 300 to 400 feet of characteristically marine deposits known as the Claggett formation intercalated between the Eagle sandstones and the Judith river beds. From the nature of the deposits constituting the Claggett formation it is evident that this return to marine conditions was not so complete as it had been in the Benton, for at intervals in the Claggett there are beds of sandstones with marine invertebrates, indicative of shallow water or littoral conditions. These are especially prevalent toward the top, where they may be regarded as prophetic of that return to terrestrial conditions which was soon to follow and which witnessed the deposition of the overlying 500 to 600 feet of non-marine deposits known as the Judith river beds. As remarked earlier in this paper the passage from the Claggett formation to the Judith river beds is in most places extremely

gradual, as is also that from the latter to the overlying marine deposits known as the Pierre or Bearpaw shales. In the first instance there is abundant evidence of the gradual replacement of marine conditions by non-marine, commencing below with littoral and brackish water deposits and terminating above with beds indicative of typical fresh water and terrestrial conditions, while in the second instance the evidence is equally conclusive of a gradual replacement of terrestrial by true marine conditions. As with the Eagle formation the Judith river beds continue for some distance to the south and east, but decrease in importance and are finally entirely replaced by marine deposits now universally referred to the Pierre or Montana group of the Upper Cretaceous. It is evident therefore that the Judith river beds in their typical development represent deposits that were contemporaneous in origin with these marine beds farther to the southeast and that they should be correlated with them.

Overlying the Judith river beds but partly contemporaneous with them in origin is the series of shales already mentioned as the Pierre or Bearpaw shales. These are true marine deposits and pass upward through the Fox Hills sandstones into that great series of brackish, fresh water and aeolian deposits aggregating from 2,000 to 3,000 feet in thickness and known as the Laramie formation. The passage from the Pierre to the Laramie is everywhere very gradual, and the evidence is so strong as to be almost conclusive that there was in this region a gradual advance of the land upon the sea resulting finally in the recovery of the entire area from the latter. Considering the enormous extent of the area which marks the present distribution of the Laramie, a very great length of time must have elapsed between that period when the first portion of this region began to appear above the level of the sea and that later period which marked the final recovery of the entire region. The length of this period is also indicated to some extent at least by the difference in the character of the brackish water faunas that in various and widely separated localities are found in beds immediately overlying the Pierre-Fox Hills[1] and which would have been contemporaneous had brackish water conditions been

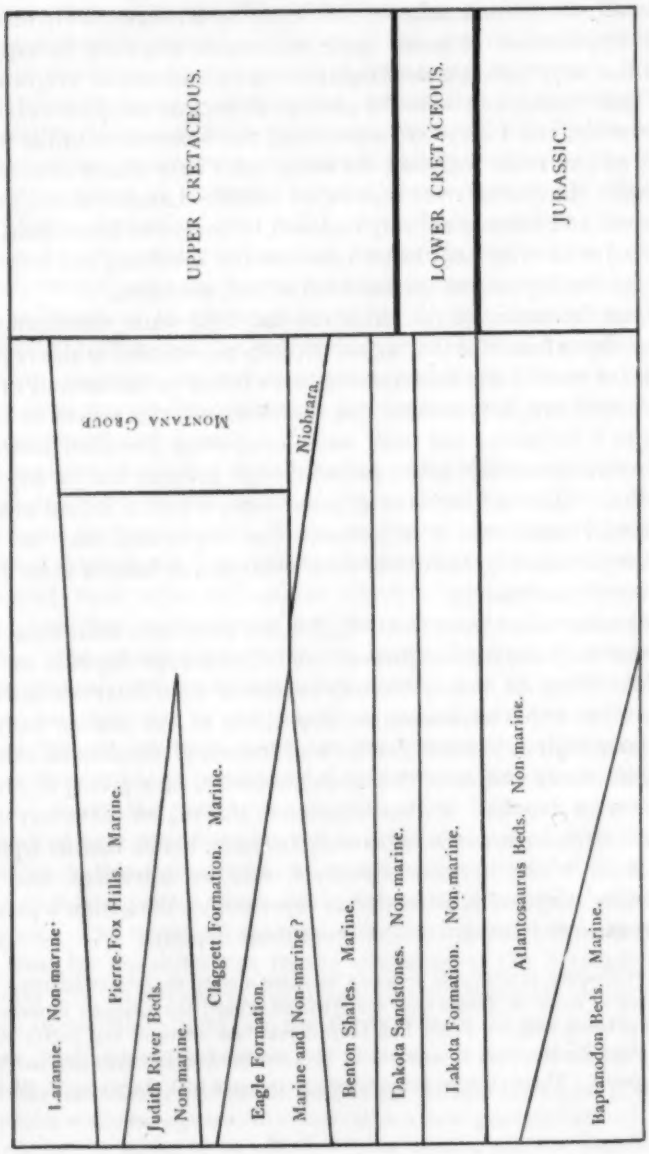
[1] This sentence was written with the idea that the Bear River fauna of Western Wyoming really belongs to the Laramie, as was once generally believed. It is now known to belong to an entirely different horizon, and this statement was agreed to by Mr. Hatcher at the time of our discussion.—T. W. S.

brought about simultaneously over this entire region, conditions however which are absolutely prohibited by any even fairly reasonable hypothesis. It seems quite reasonable therefore to suppose that the early Laramie was largely contemporaneous in origin with the later Pierre, and were the geological records complete it is not impossible, and I may say improbable, that somewhere to the westward of the 110th meridian the wedge of Pierre shales interposed between the Judith river beds below and the Laramie above would thin out and become entirely replaced by these two formations, just as the Judith river beds below pass into the overlying and underlying marine deposits to the eastward of that meridian.

From the nature of the terrestrial and fresh water vertebrate and invertebrate faunas of the various deposits represented in this region, from the base of the Atlantosaurus beds below to the summit of the Laramie above, it is evident that somewhere in this region or adjacent to it terrestrial and fresh water conditions prevailed continuously throughout this entire period though perhaps not in any one locality. Although we have at present only a partial record of such terrestrial conditions it is probable that the record may be still further perfected by the discovery of remnants at least of other non-marine formations.

From the above remarks it will, I think, have been made clear that the various non-marine Jurassic and Cretaceous deposits of our Middle West do not necessarily represent time intervals distinct from those which witnessed the deposition of the marine beds of the same region, but that marine and terrestrial conditions existed simultaneously and more or less continuously, each giving origin to its peculiar deposit. It thus happens in this region that every non-marine deposit, save the uppermost Laramie, has its marine equivalent with which by careful study it may be correlated, and the following diagram[1] is submitted as representing the author's present views as to the proper correlation of these deposits.

[1] The diagram as originally prepared has been altered slightly, as follows: The Laramie is made to extend over the Montana group; the Claggett formation is made to blend with the Pierre-Fox Hills beyond the limits of the Judith River beds; and the Niobrara is interpolated between the Benton shales and the Montana group. These changes make the diagram agree with the text.—T. W. S.


UPPER CRETACEOUS.
LOWER CRETACEOUS.
JURASSIC.
Laramie. Non-marine.
Pierre-Fox Hills. Marine.
Judith River Beds.
Non-marine.
Claggett Formation. Marine.
Eagle Formation.
Marine and Non-marine?
Benton Shales. Marine.
Dakota Sandstones. Non-marine.
Lakota Formation. Non-marine.
Atlantosaurus Beds. Non marine.
Baptanodon Beds. Marine.
Montana Group
Niobrara.

The points which it is especially desired to emphasize in the preceding pages are the following:

1. *That stratigraphic position is not the only factor to be considered in determining the relative age of geologic formations.*

2. *That an overlying deposit may have been contemporaneous in origin with that immediately underlying it instead of more recent.*

3. *That in determining the relative age and working out the phylogeny of fossil forms the geographical position at which they occur in a given formation is frequently of greater importance than the stratigraphic.*

4. *That the determination of the approximate time within a given period at which any stratum was deposited is often a more complicated problem than has been generally supposed and cannot always be estimated by its position relative to the base or summit of the series.*

5. *That every correlation should be based when possible on stratigraphy, aided by the contained fossils and an interpretation of those physical conditions attending the deposition of the beds in question.*

6. *That further studies are necessary relating to the physical conditions that prevailed and the changes that were taking place over the region occupied by the formations discussed above during the period of their deposition before we may hope to attain even a fairly satisfactory correlation.*

NOTE.

Justice to the memory of my much lamented friend, J. B. Hatcher, impels me to state my belief that had he lived he would not have published the above paper without considerable revision and alteration. The ideas that he has here attempted to express were largely suggested or confirmed by the field study of the Judith River beds in coöperation with the present writer during the summer of 1903. A preliminary statement of our results has already been published[1] and a fuller account, which will shortly appear as a bulletin of the U. S. Geological Survey under the title "Geology and Paleontology of the Judith River Beds," was written by Mr. Hatcher and myself last spring. On account of this association and of my familiarity with the region and formations under discussion, Hatcher came to me with his manuscript immediately after reading it in Philadelphia and invited criticism. At least one other friend

[1] *Science*, n. s., Vol. XVIII, pp. 211–212, Aug. 14, 1903.

in Washington also read it. Hatcher and I spent an evening in earnest, friendly discussion, at the close of which he stated that on some points he had evidently not expressed his ideas clearly, while on others his views had been modified, and that he would seek further criticism from some good stratigrapher and would revise his manuscript thoroughly before publishing it. Evidently he never found time for the revision as he did not change the manuscript in any particular.

There is certainly a lack of clearness of expression, which seems to me due to confusion of ideas, in the repeated statements that imply that stratigraphic sequence in undisturbed deposits does not necessarily mean chronologic sequence. As an example the second of Hatcher's emphasized conclusions may be quoted: "That an overlying deposit may have been contemporaneous in origin with that immediately underlying it instead of more recent." Obviously he did not mean to assert that in any actual exposure one stratum is contemporaneous with another on which it rests, or with still another above it. That would be contrary to the fundamental principle of stratigraphic and historical geology, and Hatcher repeatedly denied that he intended to express any such ideas. He meant rather that distant exposures holding the same apparent position in a formation laid down along a changing coast may not be strictly contemporaneous, and that a formation may be overlain or underlain by deposits similar to those formed simultaneously with it in another area. Thus when he says that the Pierre shales overlie the Judith River beds but are partly contemporaneous with them in origin, he refers to the fact that the Pierre shales in one area form an undivided marine formation which includes the equivalents both of the Judith River beds and of the overlying marine beds which we have designated as the Bearpaw shales. The confusion is caused by calling a part of a formation by the same name as the whole.

Mr. R. T. Hill has long ago suggested that the Dakota sandstone was a littoral formation laid down while the sea was trangressing the land from Texas, Kansas and Nebraska to the Rocky Mountain region, and that it may represent in different parts of the area a much longer time interval than its thickness would indicate. The same author gives a still better example in his discussion of the "Basement Sands" of the Lower Cretaceous, which, he says,[1]

[1] *Twenty-first Ann. Rep. U. S. Geol. Survey*, Pt. VII, pp. 132, 133.

"are undoubtedly of shallow-water or near-shore origin and represent the ancient marginal deposits of the sea as it encroached upon the land. Everywhere, next to the Paleozoic floor and conformable to its slope, this bed of sand, which seldom reaches 200 feet in thickness, persists as an apparent formation, blanketed between the underlying Paleozoic floor and overlying calcareous beds, and inclines toward the sea at a slightly greater angle than the latter.

"While these Basement sands of the Cretaceous, both in the area of outcrop and in that of the embed penetrated by the deepest wells, have the aspects of a continuous formation, they are in fact the interior margin of many formations, and were in process of deposition during a long period of time, and their successive layers are of later and later age as one descends the slope of the old Paleozoic floor."

The whole discussion from which these sentences are quoted is a clear description of an apparently continuous deposit which is not of the same age in different parts of its area, and which is thus an illustration of the principle that Hatcher especially emphasized. Such conditions are exceptional, however, and it by no means follows, as Hatcher seems to have supposed, that all, or even most, littoral and non-marine formations were extended only by accretions along their borders, and consequently that if they cover any considerable area the time required for their deposition is proportionally long, or, to quote Hatcher's words, that the time interval "should be estimated not so much by their vertical thickness as by the extent of their geographical distribution." In cases like those above cited it is usually possible to determine the true character of the deposits and to form some idea of the time interval represented by them by studying the associated formations. If a conformably overlying formation is the same throughout the area occupied and shows no change in paleontologic contents, we must conclude that the interval represented by the upper layers of the deposit in question is brief in a geological sense, although we may be convinced that the deposits at different localities were not strictly contemporaneous when measured by the smaller time units of human history. The fact that in certain cases a formation may not be strictly contemporaneous throughout its geographic extent is not denied, but the relative importance of this fact in its bearing on paleontologic and stratigraphic work is questioned. In my opinion it is greatly exaggerated in the third of Hatcher's conclusions.

Concerning two important assumptions in Hatcher's argument we could not reach an agreement: (1) That the continuance of present conditions along the Atlantic coast would result in such a succession of formations as is represented by Fig. 1; and (2) that the conditions now obtaining along this coast are comparable to any considerable extent with those of the Middle West in Mesozoic time.

The diagram (Fig. 1) was of course intended only as a crude illustration of the author's ideas. Granting that the littoral deposits might extend progressively seaward over the true marine beds, it is scarcely conceivable that the sediments laid down in brackish and fresh waters could constitute continuous formations across the entire area, nor that any great thickness of fresh water deposits could be built up above sea level on a coastal plain. Nor does it seem to me probable that even the littoral deposits laid down under such conditions would be treated as a single formation.

It is difficult to reconstruct the physiographic conditions that prevailed in the middle West during later Mesozoic time, but it should be remembered that there was then a great shallow continental or mediterranean sea, and that there were large areas so near sea level that very slight movements would bring them beneath the sea or partly or wholly drain them, so that it is probable that shallow water and non-marine conditions were often extended over large areas very rapidly. It should be remembered also that in speaking of the great geographic distribution of the resulting formations we are often dealing with their extension along a shore, or with contemporaneous deposits on opposite shores of the same sea. With such conditions it is easy to understand the many alternations of marine with non-marine formations, and it is recognized that both classes of deposits were formed contemporaneously in adjacent areas. This has made the geologic record of that region very complex, if not obscure, and it is still far from being completely interpreted.

The correlations indicated by the diagram have mostly been worked out by stratigraphic methods aided by paleontology, and agree with the present state of knowledge so far as the Upper Cretaceous is concerned. The treatment of the lower horizons is more tentative and represents Hatcher's opinions as stated in the text.

More detailed criticism and comment are unnecessary, although many minor points are subject to discussion. The whole paper is

full of suggestive ideas and again calls to mind the loss that geology has sustained in the untimely death of J. B. Hatcher. Had he lived he would have continued to make important contributions to the geologic history of the West, especially in connection with the problems concerning the non-marine formations whose importance he fully recognized and in which he was so deeply interested.

T. W. STANTON.

Washington, D. C., November 17, 1904.

THE MORPHOLOGICAL SUPERIORITY OF THE FEMALE SEX.

BY THOMAS H. MONTGOMERY, JR., PH.D.[1]

Read October 7, 1904.

It is remarkable the view should still generally obtain that the male sex is superior structurally to the female. This has resulted mainly from the fact that most writers upon sexual dimorphism have been males and, on the principle that charity begins at home, wished to give their sex all credit. Social economists in their ill-considered gleanings from Biology hold for the most part that the male is the superior, structurally and psychically, speaking of man as the "progressive" and woman as the "conservative" element of human society. But even if these terms are correctly applied, which is assuredly open to question, it does not follow that conservatism denotes inferiority and progressiveness superiority, at least from the morphological standpoint. Some naturalists share this opinion, though the facts are in patent contradiction to it; others grant the female is the superior in the lower animals, but not in the higher; most express themselves very decidedly that in the human species at least the male is the morphologically more perfect. It is a question of fundamental importance in any consideration of sexual dimorphism, especially in the valuation of the so-called secondary sexual characters. And should the common view be disproved, the relations of the sexes would show in a very different light; the male must be regarded as the inferior organism.

[1] Contributions from the Zoological Labratory of the University of Texas, No. 62.

The object of the present contribution is to deal with the subject briefly from the anatomical and embryological standpoint; considering first the Invertebrates, and lastly the Vertebrates.

1. The Invertebrate Animals.

Lamarck's collective group of the "*Invertebrata*" is of course retained to-day only for convenience; the numerous phyla which compose it differ far more greatly from each other than do any of the extremes of the *Vertebrata*.

In the *Invertebrata*, whenever there are marked structural differences between the sexes, it will be found to be a rule almost without exceptions that the male is morphologically inferior.

There are, in the first place, those numerous cases where the sexes are markedly different, in that one is much less developed than the other, *i.e.*, is the resultant of much shorter embryonic growth. Thus all the families of the *Rotatoria* so far as known, with the exception of the *Asplanchnidae* and *Seisonidae*, possess males inferior to the females in much smaller size and complete absence of the digestive system. As I expressed myself in a study of the *Flosculariidæ*, these males are arrested individuals. A more marked example is found in the Echiurid *Bonellia*, where the male is only one one-hundred-and-fiftieth the length of the female, and lacks an anal aperature; he is a degenerate, living as a parasite within the female. Similar examples occur in the *Cirripedia*. On the other hand it is seldom found that the female is embryologically more arrested than the male; such a case is that of the glowworm, however, where the male is winged but the female apterous, and in certain *Hemiptera heteroptera*. But these are arrests in external organs of locomotion, implicating less profound changes than those shown in the preceding cases.

Our case holds even for most hermaphrodites, paradoxical though it may at first appear to speak of males and females among hermaphrodites. In almost all examples of hermaphroditism it is the rule that the male and female organs of generation and reproductive cells do not mature simultaneously, but successively, as I have shown elsewhere.[1] In the greater number of these cases the male germ cells mature and are discharged first, then the female, a condition known as protandry. Here the individual is functionally

[1] "On Successive, Protandric and Proterogynic Hermaphroditism," *Amer. Nat.*, 1895.

first male, then (for a limited period) hermaphrodite (functionally male and female), lastly female; but since there is the same cycle of reproductive conditions in each individual of the species, the individual as a whole is ranked as hermaphrodite. This holds for some *Nemertini*, *Pelecypoda*, *Spongiaria*, most *Turbellaria*, *Myzostomida*, and for numerous other cases. These show the male condition to be established at the earlier ontogenetic period, before the individual has attained its complete growth; consequently the male condition is morphologically inferior to the female. There is, however, another state of hermaphroditism known as proterogyny (protogyny), with the female condition preceding the male. This is of course the reverse of protandry; it is very restricted in its occurrence, and is described only for certain pulmonate *Gasteropoda* and for the tunicate *Salpa*, cases that need reëxamination.

Hermaphroditism in the strict sense implies a condition of union of sexes in one individual, not an indifferent, non-sexual state. With this definition it is probable that hermaphroditism is a secondary condition wherever it is found, and not a primitive one. The earliest phyletic state is non-sexual, as in certain generations of some *Protozoa*. These are of anatomically distinct sexual individuals, as shown in the sporulation generations of some *Protozoa* (with micro-gametes and macro-gametes), and in most of the *Metazoa*. While hermaphroditism has appeared independently in different groups, such as the *Platodes*, the *Mollusca*, *Tunicata*, etc., where it occurs it is frequently the case that the more primitive members of the group are diœcious (with separate sexes). No Protozoan can be correctly termed hermaphrodite, but sexual or non-sexual. *Volvox* cannot be considered either Protophyte or Protozoan, but Metaphyte or Metazoan, since it contains distinct germ cells and tissue cells; it accordingly is no exception.[1] But however the hermaphroditic state may be interpreted, it stands as an indubitable fact that in most hermaphrodites the male condition occurs during the less perfect stage of the individual.

In speaking of the male as being so frequently the more arrested, more embryonic individual, corroborative examples are found in

[1] It is indeed strange that *Volvox*, at this late date of our knowledge, should still be grouped with the *Protista*. The fundamental criterion of the *Metaphyta* and *Metazoa* is not number of cells, nor their specialization, but the possession of cells which are reproductive and other cells which are not. This is the only truly important physiological distinction.

the condition known as Neotenia. This term is applied when the germ cells mature before the tissue cells have attained their final specialization; the individual is mature sexually before it is corporeally. Neotenia is found mostly (whether always, I cannot say) in males. It is not infrequent, particularly among parasites; thus in the male Gordiacean the spermatozoa may be fully mature before the animal's external enticula is completely developed. This is but another case of the male condition, *i.e.*, the essentially masculine characteristic, appearing earlier, at a more embryonic stage, than the female state appears. An increasing acceleration (in the sense of Cope) of neotenia would throw the male condition further back into the ontogeny, and could lead to the formation of embryonic males, such as in the *Rotatoria*, etc.

There next comes up for consideration an array of forms where there are no well-marked secondary sexual differences, *i.e.*, differences apart from those furnished by the reproductive systems, and where the sexes are separate. These are found mostly in the lower *Invertebrata*; most *Nemertini* (but *Carinella* with distinct coloration of the sexes), most *Hydrozoa*, *Scyphomedusæ*, *Echinodermata*, *Enteropneusta*, most dicœcious *Mollusca* and *Annelida*. Absence of secondary sexual differences is here correlated with aquatic life, fertilization of the germ cells without copulation, and relative simplicity of the genitalia. The latter in each sex consists of gonads, regions of localization of the germ cells known as testes and ovaries, and comparatively simple efferent ducts (or no preformed ducts). Accordingly, the testes and ovaries may be essentially alike, as simple sacs in the *Hydrozoa* and *Nemertini*, or surfaces in the *Polychæta*. When this is the case, and in the absence of secondary sexual differences, we cannot say which sex is morphologically the more advanced; but there is no evidence that the male is the superior. In the dicœcious *Mollusca* the reproductive organs of the female are the more complex, in the presence of various glands concerned with the formation of egg envelopes, so that in these forms the female is the more perfect.

In the large groups of *Nematoda*, *Gordiacea*, *Crustacea*, *Arachnida*, *Insecta*, progoniate and opisthogoniate *Myriapoda*, there are generally present secondary sexual differences as well as differences in the genitalia. In the *Gordiacea* the male is smaller than the female, and sometimes with greater specialization of the cuticular protuberances; but the female has more complex reproductive

organs—glandular organs not present in the male, ovaries with lateral diverticula, while the testes are simple tubes. Among the diœcious *Nematoda* the male is always the smaller, with copulatory spicules and a bursa not represented in the female; also the testes are usually impaired, a higher condition, *i.e.*, one involving more modification, than the condition in the female where there are paired ovaries. On the other hand the female is larger, with the genital ducts more complicated and with a receptaculum seminis; and unlike the simpler male condition where the genital ducts open into a cloaca, the female shows the higher morphological state of a separate aperture for the reproductive ducts (with the single exception of *Cloacina*). In both these groups, then, the female appears structurally more advanced. In the group of *Insecta*, *Arachnida*, *Crustacea*, *Opisthogoneata* and *Progoneata* we find forms that in many respects appear the most specialized of all the Invertebrates (not excluding the *Tunicata*). They are all essentially terrestrial forms, for there is good reason to conclude with Simroth[1] that even the *Crustacea* arose from ancestors that lived upon the land, or at least in very shallow water, though most of the modern representatives are aquatic. In these annulate groups, contrary to the groups considered in the preceding paragraph, we find the association of terrestrial life necessitated thereby an intimate copulation process and notable differences in the reproductive organs, also secondary sexual differences. In these forms the male is almost always smaller than the female, notably so in many *Araneæ* (particularly of the family *Argiopidæ*). The only exceptions to this rule that occur to me are a few beetles and certain *Hymenoptera*. The male may be more complex than the female in the possession of clasping organs, and sometimes in the more complete development of sensory organs. So in the ants and flies particularly the compound eyes are frequently larger in the males, and sometimes differ from those of the female in being confluent (a secondary condition). The most important olfactory and tactile organs of Insects, the antennæ, are frequently larger and more complex in the males, as shown especially in the case of the Moths; and in the Spiders the special tactile organs, long hairs, are in some cases relatively and even absolutely larger in the males. Then it is well known that in these forms the male differs frequently in external form, and often is more brightly colored than the

[1] *Die Entstehung der Landtiere.* Leipzig, 1889.

female—frequently a morphological character, as in the case of all metallic, non-pigmental colors. In these groups then the male may be the morphological superior in the possession of clasping organs or greater development of sensory organs, or of external modifications of form and structural coloration.

But we must recollect that special clasping organs are not general; they are found mainly among the *Crustacea*, by no means in all of them, and usually in correlation with the lack of an intromittent organ. With the development of an intromittent organ, which attains the greatest complexity among all animals in the Insects and Spiders, special clasping organs are rarely found. When they exist they are for the most part comparatively simple modifications of already existing structures, usually limbs. Accordingly the possession of clasping organs is a character of little morphological import.

In regard to the point that the males of these groups are sometimes superior in sensory equipment, every comparative anatomist realizes that sense organs are of little morphological value, because they are not conservative and are readily changed or lost. The Medusæ have more complex sensory organs than, *e.g.*, the *Turbellaria*, but no one would rank the former higher on this account. Any change of life leading toward loss of locomotion, as in sedentary and parasitic animals, is followed by degeneration of the sense organs as one of the first modifications; and in the case of subterranean and cavernicolous species, such a comparatively slight change as that from light to darkness, induces the replacement of visual organs by tactile and olfactory. Notice the loss of the lateral line system of sense organs in the case of the emergence of aquatic Vertebrates from the water to the land; or at least, according to a recent theory, their change into non-sensory hairs. That greater size of sense organs by no means induces greater complexity of the nervous system is shown by the comparison made by Forel:[1] in the male ant (*Lasius*) the compound eyes are largest but the cerebrum (supra-œsophagial ganglion) most rudimentary, while in the female (particularly the worker) the eyes are smallest but the cerebrum with the greatest number of ganglion cells. In fact we may say, in the light of phylogeny, that greater size and complexity of peripheral sense organs is a more primitive condition than that of small and less complex sense organs but more concentrated

[1] *Ants and Some Other Insects.* Translated by Wheeler, Chicago, 1904.

nervous system. Phylogenetically the peripheral nervous system, composed essentially of sensory nervous units, is the earlier, more primitive condition; while the centralized reflex-mechanism is later and morphologically higher. First the simple surface sensory apparatus, later the internal coördinating centre. As the central nervous system becomes more complex, a process denoting morphological advance, the more complex sense organs are apt to disappear or to be replaced by more numerous ones of less complexity.

It follows from these considerations for the arthropodous groups, that though in a few cases the males may be equipped with sense organs of larger size, this character by no means implies structural superiority, and especially not when it can be shown that with it is associated a less complex central nervous system. Indeed in the ant the male is decidedly inferior, with regard to the nervous system as a whole.

The other secondary differences, as those of external form and coloration, are generally to the credit of the male. But it is obvious that such characters, from their very lack of conservatism, imply little structural value.

Now let us examine in these groups of *Nematoda*, *Gordiacea*, *Crustacea*, *Insecta*, *Arachnida* and *Myriapoda*, to which might be added a number of smaller groups such as the *Acanthocephala*, the points in which the female is the superior of the male. One has been mentioned, the presence in some Insects of a better developed cerebrum. The other point is the greater complexity of the reproductive organs. As homologous in the sexes we consider ovary with testis, oviduct with vas deferens, certain mucous glands, and in some cases vagina with intromittent organ. The male usually possesses as dilations of the vasa efferentia seminal vesicles; except for these and the intromittent organ he has no structures not represented also in the female. The intromittent organ may be very complex as in most Insects and in Spiders (terminal joint of the maxillary palpus), or it may be very rudimentary and simple. Where it is complex the vagina of the female is frequently as correspondingly complex (*Diptera*, *Coleoptera*). On this account the intromittent organ cannot be regarded in all cases as evidencing greater complexity in the male; and probably when systematic entomologists employ characters of the external female apparatus as extensively as they have done the male for purposes of diagnosis, they will find the receptive apparatus of the female to be quite as

complex in many cases. Whenever there is intra-parental development the oviducts become specialized in a portion of their extent as uteri; such structures are not represented in the male. Very frequently also there are special glands for the elaboration of egg envelopes. Very generally there is in the female a more or less complex receptaculum seminis, usually with its peculiar musculature and duct, which is not found in the male. The ovaries may have the same structure as the testes. But not infrequently the ovaries are more complex than the testes, and this is shown particularly in the arthropodous forms. This follows from the necessity of the production of yolk substance for the egg cells, substance to be stored up in the egg for the nourishment of the embryo, whereas such substance is used by the sperm cells only in limited amount. The first formation of the yolk substance is an elaboration by the vitellocytes (nurse or follicle cells), which are germ cells that have lost their reproductive ability and become nutritive. These have their representatives in the testes in the cells of Sertoli, also nutritive. But the ovarian vitellocytes play a greater part in the growth of the embryo, and accordingly they are larger or more numerous. Further they are segregated to form particular chambers of the ovary, so that the nutritive and reproductive cells occupy different places within the ovary. This is the case in the *Rotatoria* and some *Crustacea* (*Branchiopoda*), and in the Insects, where the egg-tubes that compose each ovary have each a terminal chamber of vitellocytes (*Hemiptera*), or vitellocyte chambers alternating with egg-cell chambers (*Coleoptera*). These are all specializations in the arrangement of the nurse cells which mark the ovary as being a more complex structure than the testis. Then there is found in the female of many Insects an apparatus for oviposition, known as the sting or ovipositor, often of high degree of complication, involving parts of two (or more?) segments; this is entirely absent in the male. The female usually guards and protects the young, sometimes with the development of a brood chamber (some *Crustacea*); that is only exceptionally the case with the male, and sometimes, as in the hemipteron *Zaitha*, he is forced by the female to carry the eggs against his will. But the males of the *Pycnogonida* carry the young.

From this rapid survey of some of the facts of sexual dimorphism, we find the supposed excellence of the male to consist in what are mainly unimportant morphological characters, of which the (not

universal) possession of an intromittent organ is perhaps of the most weight. Beyond this the male may possess clasping organs, in a few cases have larger sense organs, and show brighter or more contrasted coloration, and sometimes be more varied in external form. This is all he has to show in the claim of superiority. While the female possesses an internal reproductive apparatus which is generally of much greater complexity than that of the male, and sometimes a central nervous system of higher specialization, a condition which probably will be found to be general in all those numerous cases where the female carries out the chief cares of maternal solicitude for the young. And almost without exception the female is larger than the male, a character of some structural value, because it implies, *ceteris paribus*, a longer or intenser process of embryonic development. When either of the sexes is rudimentary in comparison with the other, it is in almost all cases the male. All the facts point to the male being the more embryonic and less developed, and none to his being the morphologically more progressive.

Physiologically, also, the female appears the superior in most of the Invertebrates. The male Rotatorian, as I have watched him, emerges from an egg much smaller than that which produces a female, lives a day or two without feeding for the good reason that he has no digestive organs, then dies; while the much larger and more complicated female lives for months. In Insects and Spiders the male seems to be always shorter-lived than his mate, generally takes no part in the care of the young and dies immediately after impregnating the female. But the female lives on after impregnation, sometimes for months before depositing the eggs; then oviposits, often after great care for the protection of the young; not until all this is accomplished does she die. We may say that the female develops more slowly, reaches a larger size and lives longer, and this, together with her care for the progeny, classes her as the distinctly important individual in the economy of Nature.

2. The Vertebrate Animals.

When we turn to the Vertebrates the comparison of the sexes becomes more difficult, especially in the higher forms. The primary sexual characters may be considered first, then the secondary.

In the matter of the reproductive organs there is a complicated series of facts of structure, which have not yet received adequate

consideration with regard to the relative morphological status of the sexes, nor yet with reference to their bearing upon the questions of phyletic relationship. Relative simplicty and similarity of the genital organs, as in the Invertebrates, is found only in aquatic forms, and in those where there is neither intimate union of the sexes nor intra-uterine development. This condition is realized in most Fishes, *Dipnoi* and *Batrachia*.

Among the Fishes, more especially the *Teleostomi* (*Ganoidei* and *Teleostei*), the testes and ovaries are much alike in structure, usually sacs with more or less folded walls; this is also the condition in the *Acrania* (*Amphioxus*). In the *Batrachia*, particularly the *Urodelia*, the testes are more complicated than the ovaries since they are divided into lobes. In the *Sanropsida* and *Mammalia* the ovaries are no longer sacs, but solid cellular masses with follicle cells and germ cells intermingled; there is always, however, more or less of a radiate lobulation of the organ. The testes of the same forms are composed each of masses of tubules, of which the walls are made of cells of Sertoli and early generations of spermatogonia, while their lumen becomes filled with more mature germ cells. There can be no question that in the higher Vertebrates the testes are more complicated than the ovaries, the reverse of the case in the Invertebrates. But while the testis is morphologically more complex, it nevertheless retains primitive embryonic structures more than does the ovary. For the vasa afferentia, namely, of the testis, as at least the proximal portions of the vasa efferentia (these together constituting the tubules of the testis), represent persistent mesonephric tubules, the second kidney system of the embryo; these persist in only very rudimentary form in the ovary. From this standpoint the testis, while more complex, is concurrently less progressive; the ovary, though structurally simpler, has changed more in the course of the ontogeny.[1]

The gonads are primarily paired in the Vertebrates, except in the *Cyclostomata*. When in higher forms there is degeneration of one of the pair it is always an ovary, as in Birds, and never a

[1] In regard to the comparison of the testis and ovary, it becomes obvious that greater complexity of structure, or specialization, does not imply greater morphological advancement of its possessor, unless it is associated with correspondingly greater change in the ontogeny. So an extreme parasite, as *Tænia*, is structurally simpler than its free-living ancestor, though in point of phyletic change it is far more advanced. Regressive development is still development. This is an important consideration which anatomists do not always appreciate.

testis. Reduction of one member of a structural pair is always a departure from the primitive condition, hence a more advanced morphological state than retention of both members. But with the case in point this morphological difference cannot be justly thought of much value, for with the right ovary of Birds, as with one of the lungs of Snakes, the reduction is due simply to mechanical pressure inducing stoppage of the nutritive blood fluid, and not to any profound change in the growth processes.

Turning to the comparison of the genital ducts, we find the most primitive condition in the *Cyclostomata*, certain *Teleostei*, and, according to Gegenbaur, in the Selachian *Læmargus*: there are no genital ducts, but the germ cells fall directly into the body cavity (coelom), and are discharged to the exterior through abdominal pores. In the *Acrania* there are also no ducts, but the relations are less simple in that the genital products fall into the atrium (an ectodermic cavity) and from there are passed to the exterior through the atriopore. In these forms the sexes are alike in the mode of discharge of the genital products.

In all other Vertebrates there are special genital ducts, which may be considered separately for each sex.

Four kinds of genital ducts may be distinguished in the male, according to their mode of embryonic formation. (1) The segmental duct (pronephric duct, duct of the earliest kidney system, the pronephros) persists as the urogenital duct, as the common duct of testes and kidneys. This is the most usual condition, and is found in all the *Amniota* (Reptiles, Birds, Mammals) and *Batrachia*, all the *Selachii* except *Læmargus*, in *Lepidosteus* and *Acipenser*. In all these cases a Müllerian duct is laid down, but either remains embryonic or disappears more or less completely. (2) A direct backward growth of the testis itself is the genital duct: most *Teleostei*. (3) An open groove of the peritoneum serves as a genital duct: *Polypterus* and *Amia*, according to the description by Jungersen.[1] (4) In *Protopterus* a tube formed within the testis is the sperm-duct, and this unites with the persisting posterior end of what is considered a Müllerian duct.[2] Of these kind of ducts the last three are much more alike among themselves than is any of them to the first kind. It follows that for all gnathostomatous Vertebrates, except some *Teleostomi Læmargus* and *Protopterus*,

[1] *Zoolog. Anzeiger*, 1900.

[2] According to the account by W. N. Parker.

there is in the male a common urogenital duct, the segmental duct, which is a duct persisting from a very early stage of the embryo.

In the female of gnathostomatous Vertebrates but two kinds of genital ducts are found. (1) The oviduct is a direct backward growth of the ovary: *Lepidosteus* and most *Teleostei*. (2) The oviduct is a Müllerian duct, separate from the ovary and from the segmental duct. This may arise as an off-splitting from the ventral side of the segmental duct (most *Selachii*), but it more usually develops independently of the latter as a fold or ingrowth of the peritoneal epithelium (*Batrachia*, *Amniota* and possibly *Dipnoi*). In the female there is accordingly never a urogenital duct, but the oviducts are separate from the ureters. Further than this, while the vas deferens of the male usually possesses dilations in the form of seminal vesicles, also a prostrate gland, the oviducts are much more specialized whenever there is intra-parental development of the young. For the oviducts, besides the possession of special glands, have very complicated dilations, the uteri, much more specialized than the seminal vesicles; and in most of the Mammals the oviducts are fused for a great portion of their extent, so that in the place of paired uteri there is but a single one—a further advance beyond the male condition. The uterus is not only a receptacle for the young, but a complicated nourishing apparatus, with recurring profound morphological changes. Even in some *Teleostei* (*e.g.*, *Zoarces*) uteri may be present, though most species of this group are oviparous. The complications of the female reproductive ducts are induced by viviparity.

From this comparison of the ducts of the reproductive organs, it follows that in respect to these structures the female is morphologically the more advanced. The most important fact is the embryological one that in the male there is generally a persisting urogenital duct, in the female never a urogenital duct but oviducts separate from the ureters.

With regard to other differences in the sexual organs, the most important is the relative position in the body of ovaries and testes. Both arise in gnathostomatous Vertebrates as parallel longitudinal ridges of the peritoneum, close to the dorsal mesentery. Of these ridges only a portion fully develops, the remainder becomes arrested. An ovary is a growth at about the middle of such a ridge, a testis at a point of the ridge somewhat further back. Both ovaries and testes retain their abdominal position in most Verte-

brates. But in the higher Mammals the testes move from this position (*descensus testiculorum*), at least periodically (*Rodentia*), into an external sac, the scrotum; morphologically speaking they are still, however, intra-peritoneal. This is of course a change without parallel in the female. But in those forms where this condition obtains the female shows a structural advance which quite balances the *descensus testiculorum*, namely, complex mammary glands. These are groups of enlarged cutaneous glands, usually with complicated ducts of discharge; in the male they do not advance beyond the embryonic condition and are rarely functional. The intromittent organ of the male attains its greatest complexity in certain *Teleostei*, *Reptilia* and the higher *Mammalia*, and then is always more complex than its female homologue, the clitoris. But in the Vertebrates it is never as complex a structure as in Insects and some Mollusks, and is hardly to be considered more specialized than the clitoris and vulva considered together. Special clasping organs of the male are infrequent (*Selachii*, *Anura*). The female, on the other hand, has in some cases brood chambers for the carriage of the young, as the pouch in the Marsupial Mammals and the skin of the back in the toad *Pipa*; the mouth cavity is of use in the Viper for protection of the young. It is more rare for the male to care for the young, and to have special structures for this purpose, but such cases are found in the abdominal pouch of the teleostean *Sygnathidæ* and the oral cavity of certain *Anura*.

The foregoing facts show that the genitalia of the male and female are essentially alike in the *Acrania* and *Cyclostomata*. In most *Teleostei* they are also alike, except that the male sometimes possesses an intromittent organ. But in most higher forms they are markedly dissimilar, and we can conclude that as a rule the female is morphologically more advanced in the point of gonads, genital ducts, and apparatus for the protection or nursing of the young. From the standpoint of the reproductive organs the female is clearly the superior.

Most investigators of mammalian embryology explicitly hold that the male represents an individual advanced beyond the condition of the female. They adduce the facts that the external genitalia are at first alike in the sexes, then while the clitoris remains small the intromittent organ continues to grow, and while the ovaries retain their original position the testes descend into the scrotum. But these are relatively small differences in comparison with the others we have reviewed.

The other characters in which the males of Vertebrates differ from the females are secondary sexual. Sometimes such external differences are very slight or not perceptible, as in many of the Fishes, Birds and urodelous *Batrachia*. In most of the group, as we found for the Invertebrates also, the male is smaller; this is the case in the *Acrania*, *Cyclostomata*, *Selachii*, most *Teleostomi*, *Dipnoi*, most *Batrachia*, even in most *Reptilia*. In most Birds where there are sexual differences in size the male is the larger (but the female is in certain species of *Falconidæ* and *Scolopacidæ*), and in Mammals too the male is generally larger. This is an important difference, particularly when it implies a longer growth period and slower attainment of maturity, as in the Primates; we shall recur to this point. When there occurs dichromatism, it is the male that has the brighter or the more contrasted colors, as it s the male that possesses more marked integumentary structures, such as odoriferous glands, combs, plumes, greater development of feathers and hair, spurs, etc. But the greater intensity of coloration does not always denote morphological advance, for frequently the colors are not structural (diffractive) ones. And the greater complexity or size of integumentary structures is well known to be a character of little morphological importance, because of the lack of conservatism of such parts, their ready susceptibility to change. Among closely related forms, as in some families of Birds, we may find a species in which the sexes are externally alike in color and plumage, and another species in which they are quite dissimilar in these respects. In the Reindeer the cow has antlers as well as the bull, contrary to the condition in other deer. It is only rarely that the differences of the male are of greater morphological import, as in the different form of skull in the male salmon. We may decide from another point of view that secondary sexual characters must be estimated as of little value, because they have not even the worth of a species diagnostic, being not representative of all the individuals of a species. Accordingly, such secondary sexual differences are of too small worth to occupy much attention in the matter of comparing the sexes.

We have now briefly compared the sexes by the standards of the structure of the reproductive organs and of the secondary sexual differences. We have found that while the female usually shows more advancement in the reproductive organs, the male evinces more in secondary sexual characters. Obviously it becomes a question of which of these characters is the more important.

The only secondary sexual character of morphological importance is that of bodily size, as we found in discussing the Invertebrates; it is the only one at all commensurate with anatomical differences in the genitalia. Its importance lies in the fact that greater size of one sex means a longer or more intense growth, greater continuation of development. This is the more evident where greater size is associated with longer time before the attainment of reproductive maturity. To be sure this must not be interpreted to mean that longer embryonic growth period is always to be construed as implying higher morphological rank, for the Elephant takes longer to mature than does Man, yet the Elephant is decidedly lower in the phyletic scale; so, also, some Reptiles take a longer time than many Mammals. But within the same species, where one sex grows larger than the other it is, *ceteris paribus*, a sign of distinct morphological advance beyond the other.

Now in most of the lower Vertebrates (most Anniotes and Reptilia) the female is the larger, and at the same time usually the more advanced with regard to the reproductive organs; the male shows his superiority only in unimportant integumentary characters. For such Vertebrates it is very plain that the female is structurally superior. But in most Birds and Mammals (much more rarely in lower forms), while the female is still more advanced in the structure of the genital organs, the male is usually the larger—a condition rare among animal groups treated as a whole. Is then the female still morphologically superior in these forms, or are we to consider that the relation has reversed itself so that in the highest forms the male has become the morphological superior? It is the question of the relative worth of the two characters: greater complication or embryological advancement of the reproductive organs or greater bodily size implying a longer period of development. Or we may state it: the female is embryologically the superior in respect to the reproductive organs, the male in regard to the other organs of the body—which of course is directly correlated with the greater part that the female takes in the process of procreation. While different morphologists might estimate the value of these characters differently, I am inclined to judge the greater embryological advancement of the reproductive organs to be a condition of more morphological importance than greater bodily size.

So we reach the conclusion, that the female is clearly the super-

ior, from the standpoint of morphological advancement, in the Invertebrates and the Lower Vertebrates; and still superior, but in less degree, in the higher Vertebrates. This is certainly the opposite of the view of most naturalists, but to my mind there can be no other inference from the facts.

University of Texas, September 22, 1904.

Stated Meeting, October 21, 1904.

President SMITH in the Chair.

The death was announced, at Philadelphia, of Rev. Jesse Y. Burk, on October 18, aet. 64.

Dr. George T. Moore, of the Department of Agriculture, Washington, read a paper on "A New Method for the Purification of Water Supplies."

Stated Meeting, November 4, 1904.

President SMITH in the Chair.

The death was announced of the Marquis de Nadaillac, at Château de Rougemont, St. Jean Froidmentel (Loir-et-Cher), on October 1, 1904, aet. 87.

The following papers were read:

"The Behavior of the Lowest Organisms," by Dr. Herbert S. Jennings.

"Electrolytic Calcium," by Joseph H. Goodwin.

Stated Meeting, November 18, 1904.

President SMITH in the Chair.

The death was announced, at Bethlehem, Pa., on November 16, of Dr. Thomas M. Drown, aet. 62.

Prof. Bailey Willis, of the Carnegie Institution, read a paper entitled "By Courtesy through China."

ELECTROLYTIC CALCIUM.

[*Contribution from the John Harrison Laboratory of Chemistry.*]

BY JOSEPH H. GOODWIN.

(*Read November 4, 1904.*)

Metallic calcium can be easily made in large quantities as shown by the following experiments which required only a short time and simple and easily constructed apparatus. The method used was the electrolysis of fused calcium chloride with a hollow cylindrical anode vessel of Acheson graphite (Fig. 1). At first the bottom was

Figure 1.

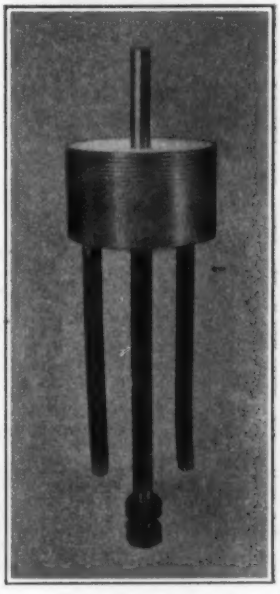


Figure 2.

closed by a smaller iron cylinder insulated from the graphite by asbestos, cooled by circulating water in it and having an iron rod projecting upward through its centre to form the cathode (Fig. 2). This was discarded because the calcium (1) often short-circuited the furnace by the formation of spongy metal, (2) was obtained in small pieces, (3) was difficult to remove, and (4) was surrounded

by molten calcium chloride with which it combined, greatly lowering the current efficiency. In connection with this form of cathode an attempt was made to use a cylinder of fine iron gauze to collect

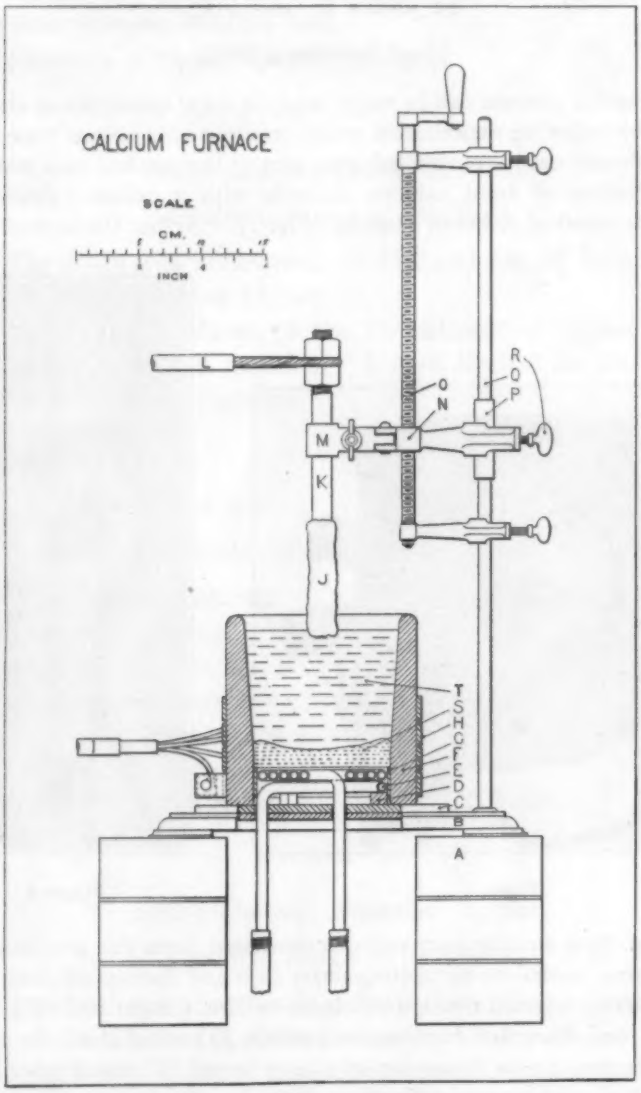


Figure 3.

and retain the molten calcium, like the nickel gauze in the Castner sodium furnace, but the long continued action of 225 amp. would not fill this gauze with calcium because it presented a large surface for the rapid recombination of the calcium: $Ca + CaCl_2 = 2\ CaCl$.[1] The formation of calcium and chlorine almost ceases and active reaction and circulation are seen to take place in the molten electrolyte.

In the satisfactory furnace (Fig. 3) the bottom of solid calcium chloride was maintained by the cooling effect of a copper coil (E, Fig. 3 and Fig. 4) through which water was circulated. This coil was insulated from the graphite by asbestos, but a Weston milliammeter indicated that it was carrying .17 amp. of the anode current (190 amp.); therefore, to prevent contamination of the bath by copper, a gravity cell (B, Fig. 5) was connected between the copper and the graphite and the milliammeter indicated .04 amp. flowing the other way. This very simple and efficient cooling coil was made by annealing four feet of $\frac{5}{16}$-inch seamless copper tube in a Bunsen flame, filling it with sand, plugging the ends and bending it easily into shape by hand.

Figure 4.

The new form of cathode was a $\frac{5}{8}$-inch iron rod (K, Fig. 3), dipping into the bath from above and capable of being raised or owered by the screw mechanism O. As the calcium was deposited on the end of this iron rod it solidified, due to the cooling effect of the cold upper part, the whole was gradually raised, the calcium itself conducted the current away and formed the cathode, continuing to grow in the shape of an irregular cylinder J. This is simplicity itself because it accomplishes at once—

1. A method of making cylinders of calcium up to 4 cm. diameter and of any length desired with this small furnace. (When the limit of the screw is reached the clamp M can be loosened, lowered and a new hold taken.)

2. Quick removal of the calcium from the molten calcium chloride, which is essential to maintain a fair current efficiency.

[1] Borchers, *Elektro-Metallurgie*, 1896, p. 78.

3. Oxidation prevented by a covering of calcium chloride, fine particles being deposited by the bursting of bubbles of chlorine rapidly evolved at the anode.

The furnace is shown in detail in Fig. 3, and all dimensions can be found by reference to the scale. The bricks A support the retort stand B, on which is a thick piece of asbestos C, holding by the blocks D the copper coil E well up in the Acheson graphite anode F and insulated from it by the asbestos G. The iron bands H conduct the current from the positive cable I to the graphite vessel F. The calcium grows and forms the stick J, which is started by the iron cathode K connected with the negative cable L and supported by the clamp M, which is drilled and tapped at N to receive the screw O by which it can be raised or lowered. P is a tube sliding freely on the rod Q of the retort stand, and against which R is firmly screwed to make the clamp M fairly rigid without interfering with its vertical motion. Fluor-spar covers the copper coil and fills the space about it, while the furnace is filled with calcium chloride which becomes solid at S and is kept molten at T solely by the current passing through the furnace. The whole apparatus was set up inside an empty wind furnace from which the grate bars had been removed. In this way the escaping chlorine was drawn from the room. Pure anhydrous calcium chloride was used, melted in a Dixon graphite crucible and added from time to time, but this was found to introduce much iron, aluminium and silicon from the clay binding used in the crucible, so that finally the chloride was added cold and melted by drawing an arc from the iron rod K. Thus the furnace was filled sufficiently for a run.

Fig. 5 is a diagram of the circuits. A direct current dynamo

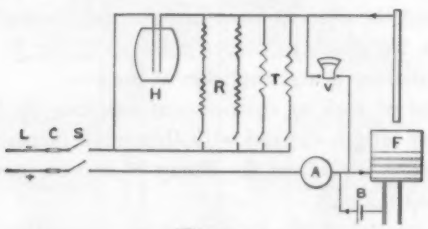


Figure 5.

supplied the current to the furnace line L at about 95 volts, having 250 amp. fuses at C and a double pole switch at S. Regulating

resistance was supplied by a barrel of soda solution H, having two ten-inch square cast iron furnace doors for electrodes and capable of carrying 75 amp., two pairs of two wire resistance frames R of 75 amp. capacity and 1 ohm resistance per pair in series, two wire resistance frames T of 10 amp. capacity and 8 ohm resistance each. A Siemens 320 amp. ammeter is indicated at A and a 150 volt Weston voltmeter at V. F is the calcium furnace and B the gravity battery to keep the copper coil from carrying any of the anode current. The anode was turned in a lathe from a six-inch length of Acheson graphite electrode six inches in diameter. Being pure and able to withstand the high temperature and chlorine without disintegration made this material by far the most suitable for constructing the furnace.

In operation the volts and amperes vary when the cathode is raised, but the following rough furnace record will give a pretty close average of the working conditions:

Run.	*Date 1904.*	*Volts.*	*Amp.*	*Hours.*	*Grams Calcium.*	*Current Efficiency.*
1	July 12	20	105		40	
2	" 14	15	160	4	200	41.9
3	" 15	14	175	8	225	21.5
4	" 16	22	125	6	150	26 8
5	" 18	19	160	6	295	41.2
6	" 21	18	180	5	150	22.3
7	" 22	19	185	4	125	22.6
Total					1185	

Taking account of the different length of runs and averaging we get for runs 2 to 7—

Average volts ... = 17.7
" amp. ... = 163.
" efficiency = 29.1%

On finally weighing the total yield of clean calcium there remained 1050 grams. Adding 35 grams for loss by oxidation, analysis and samples (= 1085 grams), the efficiency becomes

$$29.1 \times \frac{1085}{1185} = 26.6\%$$

If covered by an inverted graphite crucible the furnace can be left cold for more than forty-two hours, and then started again in a

couple of minutes without the least trouble by drawing an arc between the iron cathode and graphite anode at the surface of the solid calcium chloride which immediately melts, allowing the iron end to be immersed and moved slowly to the centre of the furnace as the zone of fusion widens until it soon extends to the graphite on all sides. The sticks of calcium obtained were of irregular shape and covered with chloride. The bright metal showed the following composition, found by an analysis of the piece used in the tension and conductivity tests:

Si	0.03%
Fe	0.02 "
Al	0.03 "
Ca	98.00 "
Mg	0.11 "
Cl	0.90 "
O (by difference)	0.91 "
	100.00 "

The product of run No. 5 is shown in Fig. 6. This piece was 56 cm. (22″) long, .8 cm. ($\frac{5}{16}$″) least and 3.2 cm. (1¼″) greatest diameter, weighed 295 grams and represented a current efficiency of over 40%. Some of the other pieces were of larger diameter. The difficulty experienced until recently in making metallic calcium was probably due to the small scale on which the operation was tried. The simple and satisfactory operation of this furnace would lead one to believe that, technically, the process would be still more efficient and easily controlled. A furnace five times as large, using about 1200 amperes, would require about 8 volts, and the screw mechanism could be electrically controlled, keeping the current constant and the product perfectly uniform, as the rotary furnaces of the Union Carbide Co. are controlled. A water-cooled shield might be necessary to cool the large calcium cathode as it was drawn from the bath. The two essential conditions of operation are—

1. Rapid withdrawal of the metal formed to increase the yield and minimize recombination.

2. Narrow temperature limits. The bath must be hot enough to deposit the metal molten, not spongy, and cool enough to let it congeal upon the cathode and be raised without breaking off.

To clean the metal most of the chloride was broken off with a

hammer and the rest dissolved off by leaving the pieces in 95 per cent. alcohol over night. Some hydrogen was evolved but the loss due to this cause was not very great. To keep the metal for a long time it was put under oil, dipped in melted paraffin or simply put in a dry stoppered bottle.

An attempt was made to fuse several pieces into one big stick. A two-foot length of one-inch iron pipe was threaded at both ends

Figure 6.

Figure 7.

and a cap screwed firmly on one end. The inside was cleaned with dilute sulphuric acid and washed with water, alcohol and ether, and in it were placed about 300 grams of clean pieces of calcium. The whole was heated in a wind furnace to a bright red heat, and on looking down into the tube one could see the red-hot molten metal which was quite fluid as shown by a thick iron wire used as a poker. The upper cap was then screwed on, the tube drawn from the fire,

its lower end hit smartly on the cement floor several times, after which the tube was quickly cooled in water. The lower cap was broken off and the walls of the tube cut lengthwise in the milling machine. When torn apart the two halves, split down the centre, displayed a most beautiful mass of large, reddish-violet, cubical crystals (Fig. 7). There was much speculation as to the composition of this peculiar "compound" until the following analysis showed it to be over 90 per cent. calcium:

Gangue	0.03%
SiO_2	0.77 "
Fe_2O_3	0.46 "
Al_2O_3	0.77 "
Ca	91.28 "
Mg	0.11 "
Cl	1.28 "
C	trace
N	trace
O (by difference)	5.30 "
	100.00 "

The crystals showed a specific gravity of 1.5425 at 28.1° C. In water they evolved hydrogen with an oder of acetylene. Carbon was probably extracted from the iron melting tube, which reaction may be of technical importance for converting pig iron into steel, and the power of calcium to combine with and remove sulphur and phosphorus are very important as is also its strong reducing action on organic compounds, the reaction being more easily controlled and less dangerous than with metallic sodium. These crystals were quite soft and were hammered as thin as paper, often exploding with a slight flame under the impact of the hammer. When filed or cut they showed a brilliant metallic lustre, being not as pure a white as silver but slightly yellow. The solid metal at times has this same slight yellow tint. The crystals near the top of the tube evolved ammonia with water, showing that they had combined with the nitrogen in the melting tube.

The solid metal can be worked like other metals and is much more stable than imagined. It can be heated red hot continuously in a triple Bunsen flame without igniting, but at this temperature its texture is like clay and it can be easily squeezed apart with the tongs, sometimes igniting at the edges and burning feebly till the

lime formed smothers the flame. When sent whizzing through the air against asbestos, bricks or cement it burns violently with a brilliant white light like magnesium and leaves a streak like antimony. It is not hardened by heating red hot and plunging into water. At 300°–400°C. it is as soft as lead and the irregular sticks can be easily hammered on an anvil, rolled, swaged or worked into any shape whatever by simply heating from time to time. When cold a bright calcium surface becomes dull rapidly in ordinary air, but if hot the metal can be brightened with a file or polished in the lathe with emery cloth and will remain bright as long as it is hot. About 300 grams of fine bright specimens were prepared as follows: A glass cylinder and its stopper were put in an air bath, gradually

Figure 8.

heated and kept at 150° C. The calcium was kept hot on a stove plate and the pieces polished one at a time and put in the cylinder in the air bath where they kept bright till all were polished. A little paraffin was rubbed around the stopper and the cylinder closed. In this dry air they have lost none of their lustre and their bright surfaces are as distinctly metallic as any other metal. Fig. 8 shows the cylinders of crystals and solid metal and a six-inch stick of polished calcium.

Specific Gravity.

The density of oil was determined by the density bottle and from weighings of a bright piece of calcium in air, and in this oil its

specific gravity was found to be 1.5446 at 29.2° C., which is compared with some other metals in the following table:

Li	.59	Sb	6.76	Ag	10.505
K	.87	Zn	7.00	Pb	11.38
Na	.97	Sn	7.35	Hg	13.58
Rb	1.52	Fe	7 93	Au	19.258
Ca	1.54	Co	8.55	Pt	21.5
Mg	1.74	Cu	8.89	Ir	22.4
Al	2.68	Bi	9.82	Os	22.5

Conductivity.

On the milling machine a piece of calcium about 10 cm. long was accurately finished on the sides and measured 1.43 × 1.02 cm. It was imbedded in a block of wood with a mercury cup at each end and connected through a 15-ampere Weston ammeter, variable resistance and switch with storage batteries. Sharp brass potential points near the ends led to a large, very sensitive, horizontal D'Arsonval galvanometer whose deflections were read by a telescope and scale. The value of the galvanometer deflections in volts was obtained by using a standard low resistance in place of the unknown piece of calcium. The average of several readings gave the resistance between points 7.2 cm. apart 19.4 microhms at 30° C., and 26.7 microhms at 123° C. in a bath of hot paraffin.

Solving the equations

$$R_{30} = R_0 (1 + 30\alpha) = 19\,4$$
$$R_{123} = R_0 (1 + 123\alpha)$$

we get the resistance at 0° C.

$$R_0 = 16.94 \text{ microhms}$$

and the temperature coefficient

$$\alpha = .00457.$$

Hence the specific resistance at 0° C.

$$= \frac{16.94 \times 1.02 \times 1.43}{7.2} = 3.43 \text{ microhms per cm. cube.}$$

At the mercury cups calcium slowly formed a voluminous amalgam.

In the table below these values for calcium are placed in Sir Roberts-Austen's relative electrical conductivity table and show

that calcium is the fifth best conductor, being surpassed by silver, copper, gold and aluminium, if wires of equal diameter and length are compared, but for wires of equal weight and length the order is entirely different, calcium being second and exceeding silver by 67 per cent., copper by 62 per cent., gold by 86 per cent., and aluminium by almost 20 per cent. This method takes into account the specific gravity of the metals and gives the following order of conductivity: sodium, calcium, potassium, aluminium, magnesium, copper, silver, gold, etc. With purer metal still better results are to be expected.

Metal.	*Spec. Res. 0°C. Microhms per cm. Cube.*	*Temp. Coef.*	*Relative Conductivity.*	
			Similar Area and Length.	*Similar Weight and Length.*
Ag	1.55	.00377	100.	32.5
Cu	1.59	388	97.6	37.5
Au	2.02	365	76.6	13.6
Al	2.45	390	63.	80.4
Ca	**3.43**	**457**	**45.1**	**100.0**
Mg	3.92	.....	39.4	75.5
Na	5.04[1]	438[1]	31.4	115.
Zn	5.22	365	29 6	14.5
Cd	6.34	.....	24.4	9.7
K	7.01[1]	581[1]	22.1	86.8
Co	9.15	.....	16.9	6.8
Fe	10.6	117	14.6	6 3
Pt	10.7	247	14.4	2.3
Sn	10.7	365	14.4	6.7
Ni	12.0	.....	12.9	5.0
Pd	12.8	.....	12.1	3.6
Th	16.9	.....	9.1	2.6
Pb	18.4	387	8.4	2.5
As	33.1	.....	4.7	2.8
Sb	43.1	389	3.6	1.8
Hg	94.0	93	1.6	.4
Bi	110.	.....	1.4	.5

An attempt was made to find the specific heat of calcium, but the results are too poor for publication.

Tensile Strength.

From the piece of calcium used in the conductivity test a specimen was cut with a hack-saw, finished to .458 x .135 cm. and marked off into half centimeters. The upper end was gripped in a

[1] A. Bernini, *N. Cimento*, 6, pp. 27 and 294, 1903.

vise, and to a hand-vise clamped on the lower end a 50-lb. weight and empty bucket were freely hung. Sand was poured into the bucket and the specimen broke with a total load of 83.5 lbs., showing a tensile strength of 8,710 lbs. per sq. in. or 612 kg. per sq. cm. The elongations in the middle

1 cm. = 23. %
2 " = 15.
3 " = 11.
5 " = 6.6

The following table shows the comparative strength of some metals:

Metal.	*Ultimate Tensile Strength.*	
	Lbs. per sq. in.	*Kg. per sq. cm.*
Ag	41,000	2,880
Pt	32,000	2,250
Mg	30,000	2,110
Cu	24,000	1,690
Au	20,000	1,410
Al (cast)	15,000	1,050
Ca	**8.710**	**612**
Zn	7,500	527
Sn	4,600	323
Pb (sheet)	3,300	232
Bi.	3,200	225
Sb	1,000	70.3

Calcium is harder than sodium, lead or tin, almost as hard as aluminium, but softer than zinc, cadmium or magnesium.

The activity with which strontium and barium recombine with their chlorides makes them more difficult to produce. Their production was not tried in the furnace just described. There are many interesting things to be learned about the alkaline earth metals—their isolation, purification and action on gases, solutions, organic compounds, salts, oxides and metals. The question of alloys is a broad one; some might be found of special value because of their electrical conductivity, strength or extreme lightness, calcium being only $\frac{1}{4}$ as heavy as the light metal aluminium. The manufacture of cyanide and peroxide were uses found for metallic sodium, and in like manner uses will be found for calcium. It should be of use in the steel industry and for reduction purposes.

University of Pennsylvania.

Stated Meeting, December 2, 1904.

President SMITH in the Chair.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The death was announced of Dr. Helen Abbott Michael, at Boston, on November 29, 1904.

The following papers were read:

"Mineral Symmetry," by Prof. Amos P. Brown.

"The Origin of the Markings of Organisms due to the Physical rather than to the Biological Environment," by Prof. Alpheus S. Packard.

THE ORIGIN OF THE MARKINGS OF ORGANISMS (PŒCILOGENESIS) DUE TO THE PHYSICAL RATHER THAN TO THE BIOLOGICAL ENVIRONMENT; WITH CRITICISMS OF THE BATES-MÜLLER HYPOTHESES.

BY ALPHEUS S. PACKARD, LL.D.

Read December 2, 1904.

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19. Thayer's law and his experimental proofs.

20. Experiments on the obliteration of bars and spots with Bradley's color-wheel.

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1. Introduction.

In this essay I have first attempted to bring together the more important published facts or results concerning the supposed destruction of butterflies by birds, together with others gathered from correspondents, with a few observations of my own. At the outset it should be observed that protective coloration, a generally accepted fact, is quite a different matter from protective or Müllerian mimicry. Soon after the subject of protective mimicry was broached I found myself unable to accept the views of Bates, Müller, Wallace and others, and offered[1] the suggestion that the mimickers have survived simply by reason of their resemblance to the more abundant forms which appeared as the old-fashioned or primitive types were on the wane or dying out. In my little books I expressed the belief that the resemblance in pattern and color between insects belonging to different groups is probably due to causes more fundamental than natural and sexual selection, and possibly reaching farther back in geological time than the present period.

[1] *Half Hours with Insects*, 1876, pp. 281, 286; also *Zoology for High Schools and Colleges*, 1879.

Thus a day-flying brightly-colored broad-winged moth such as the East Indian *Callamesia midama* "mimics" the blue Euplœa butterfly, and the species of Chalcosia mimic, in the shape and markings of their wings, certain butterflies of the family Heliconidæ. It occurred to me that the brilliantly colored day moths, which are evidently of earlier origin than butterflies, may have been preserved from their resemblance to butterflies. But this is supposing that butterflies serve as a staple food of insectivorous birds, which now seems to be by no means the case, butterflies in reality appearing to enjoy a peculiar immunity from the attacks of birds.

Since looking more carefully into the subject and realizing the slight basis of fact which underlies the original hypotheses of their propounders, and that the importance of Bates-Müllerian mimicry in species-making has been unduly magnified by more recent writers, I have felt more strongly inclined than ever to discard these hypotheses and to look for a broader and better founded theory or explanation of the fact of the recurrence of similar colors, designs or patterns in butterflies and in animals of other groups.

It is now evident that protective mimicry in the case of butterflies, supposed to result from the attacks of birds, is not an isolated series of facts, to be explained by the struggle for existence of butterflies resulting from the attacks of birds, but that the same phenomena occur in a number of other classes of animals. Thus antelopes may be said to mimic zebras; the spotted leopard of the Old World is marked like the jaguar and ocelot of the New World, their habits and environment being the same; shallow water fishes, both those abounding in the shoal waters of coral reefs, as well as the fresh water minnows, perch, darters, Lycodes, cottoids, etc., and the poisonous Elaps, as well as the harmless species marked like them—this similarity of markings and patterns in animals exposed to direct sunlight, or living under the same conditions of life, is due not so much to Bates-Müller mimicry as to what we call convergence, or the result of adaptation to similar physical environments or backgrounds and to similar modes of life.

It may be questioned whether the same physical agencies which have painted sun-loving animals have not also ornamented the petals or corollas of flowers with bars, stripes, lines and spots, the patterns being subject to almost infinite variation.

Thus the subject has entered on a new phase, and what has been understood as protective mimicry, in the sense of Bates and of

Müller and their followers, has a precarious basis. There are, to be sure, interesting coincidences, but a coincidence is not a *vera causa*. Natural selection as such is inadequate as an originating cause, though it operates as a preservative agent. The markings apparently did not originate in single variations, liable to be swamped by crossing, but whole masses of individuals, all those inhabiting a given area with its peculiar features, have been affected alike. The causes were not primarily biological and limited, dependent on sporadic and individual variations, but physical and widespread, occurring in different regions.

It will also be seen that the Bates-Müller hypotheses are seriously undermined by the fact that the wings of insects were, as early as the Carboniferous period, striped or barred and spotted, long before birds ever appeared.

Mr. Abbott H. Thayer, with the keen powers of observation of the artist as regards the effects of light and shade, hits upon the right explanation when he claims that protective coloration makes the animal "cease to appear to exist at all," and that "animals are painted by nature darkest on those parts which tend to be most lighted by the sky's light," and *vice versa*. He likewise points out that what naturalists call conspicuous colors, *i.e.*, strong arbitrary patterns of color, "tend to conceal the wearer by destroying its apparent continuity of surface. Thus the mallard's dark green head tends to detach itself from its body and to join the dark green of the shady sedge, or the ruby of the humming bird to desert it and to appear to belong to the flower it searches." His experiments capitally illustrate and confirm his views.

Steinach's earlier experiments seem to conclusively prove that light and shade acting on the integument of the living frog, or its dead and dry skin, cause light and dark markings.

Pocock has clearly shown that zebras and antelopes are banded, or not, in accordance with the nature of their habitat or environment, *i.e.*, whether they are confined in their range to forest regions or to the bush or to open plains.

It thus appears to be fairly well established that the markings of the skin and scales or feathers and hair of animals are due to the effect of the sun's light, or its absence, on the pigment in the integument, or its covering.

The biological cause suggested by Bates and by Müller, and so strongly advocated and extended by their followers, now appears to

be quite inadequate and misleading. On the other hand the physical causes we here advocate must be our main reliance in a thoroughgoing and satisfactory explanation of the phenomena of protective coloration. There is nevertheless need of much additional observation and experimentation.

2. Facts against the Bates-Müller Hypotheses, from Observations made in North America.

For the first time in my life, having for over forty years observed and collected insects, though by no means constantly in the field, I actually saw a bird chase a butterfly. It was with great interest that I watched the procedure both of the bird and butterfly from the piazza of my summer cottage on the shores of Casco Bay, Me., at noon of a bright sunny day early in July, 1901. The aggressor was a black-throated green wood-warbler, the quarry a Pieris, apparently *Pieris rapæ*, then not uncommon about the house. The warbler was seen to dart swiftly after the butterfly, whose flight is very erratic and unsteady. It disappeared after flying a few yards, and as the bird kept on alone in its course, I had good reason to believe that it had caught and swallowed the butterfly. Prof. H. H. Wilder, then living in the next house, at about the same date actually observed one of these warblers eating a Catocala in a path. It ate the body of the moth and left the wings lying on the ground. I also saw one of these warblers chase a Catocala around an elder bush on the edge of my piazza, but did not see that the bird was successful in his pursuit.

Kingbirds were common about the house and shore, but I did not see any chase the cabbage butterflies, but was interested in witnessing one pursue a red-under-wing moth (Catocala). The moth flew in its usual very rapid and zigzag fashion, darting in this and that direction, as usual with species of this genus. The bird in vain tried to seize the saucy moth so secure in its rapid, zigzag, tumbling, headlong flight. The race was maintained for about five hundred feet; but so far as I could see, for the racecourse led directly from me, the moth escaped scot-free, the kingbird being baffled and outflown. I then realized, as must every one who watches the swift, zigzag, apparently aimless flight of any butterfly, how admirably adapted such a mode of progression is for the preservation of the species.

I might add a case which a few years ago fell under my observation when I observed in a street in Providence a small bird about the size of the English sparrow—perhaps it was one—pecking away at a large dragon fly (*Æschna grandis*). The dragon fly was disabled, could not fly. I picked it up, but the bird flew off, and was not with certainty identified.

These occurrences have led me to review the subject of the Batesian and Müllerian hypotheses and to come to the conclusion that the theories of these and of later advocates have in reality but a slight basis of fact. The two points of interest are, first, do birds to any appreciable extent, even the few species, like swallows, the European bee-eater, and our kingbird, shrike and fly-catcher, occasionally pursue and devour butterflies, *i.e.*, depend much on these lepidoptera as an article of diet? It is of course admitted that moths, as other insects, are often caught and eaten by insectivorous birds. Secondly, is the protective or adaptive coloration of butterflies and other insects due to the action of natural selection, or are the similarities of colors and of patterns of colors, so frequently observed in all parts of the world, but especially in the tropics, primarily due to simple physical causes, such as the physiological deposition of colored pigments, and the action of light and moisture?

To this end I have with some care reviewed the original papers by Bates, Müller, Wallace, Poulton and others, but to my surprise find that neither of these framers and advocates of the hypotheses in question have themselves ever actually witnessed a bird catch and devour a butterfly.

Evidence from cases observed in the United States.—We will first review the evidence from cases observed in the United States of America. The insect-eating habits of sparrows have recently been described in a very interesting and satisfactory way by Mr. Sylvester D. Judd in a recent bulletin issued by the Biological Survey of the U. S. Department of Agriculture, entitled "The Relation of Sparrows to Agriculture." Mr. Judd has made this a specialty for several years, spending a great deal of time in field work, both in the Northern and Middle States, observing the habits of sparrows. And yet he writes me, "Personally, I have never even seen a bird in the field give chase to a butterfly. The following birds, either in captivity or in the wild state, have been known to eat butterflies: the catbird, kingbird, wood pewee, purple martin, scarlet tanager,

crown blackbird, cuckoo, English sparrow, song sparrow and the migrant shrike. I do not know of a kind that feeds upon butterflies during any month of the year to the extent of one-tenth of one per cent. of its food." This is certainly a strong statement, and is based on prolonged and very thorough investigations.

Mr. L. H. Joutel informs me that he has seen the English sparrow chase, seize and devour one *Pieris rapæ* and an Orgyia. He also observed these birds running after and catching little moths and flies, and also saw a sparrow pull off the abdomen of a large moth and devour it. These birds will, in the side streets of New York, dart out into the open and apparently catch some insects, and then perch on a neighboring tree or telephone pole. The sparrow, which on the whole eats few destructive insects, is occasionally in the city very voracious. Mr. Joutel had 150 caterpillars of *Callosamia promethea* in the last stage on the shrubs in his back yard on East 117th street. In the course of a couple of hours in the forenoon the sparrows ate them all. And some Japanese *A. pernyi* worms living on his oak trees were similarly massacred.

Mr. Joutel corroborates the statement made that Lycænæ when at rest on a leaf hold the wings closed upright over the back, but the hind wings with ocellus and tail are continually moved up and down, so that the two little tails look like its antennæ and the ocelli like the eyes of the same butterfly.

In a captured Thecla he observed where pieces had been bitten out of the hind wings, as if attacked by some birds which had mistaken the hind wings for the head.

Prof. J. B. Smith writes me: "I have never observed birds chasing butterflies except once. That was some years ago and the bird was a sparrow: the victim *Pieris rapæ*."

Miss Caroline G. Soule writes: "I have seen chipping sparrows, Savannah and song sparrows catch and eat a few *V. milberti*, *P. rapæ* and *myrina* butterflies. I have seen thistle-finches attack *turnus* and *cybele*, but not eat them. I have seen dogs eat *philodice* more than birds. When it comes to moths the tale is quite different. *Clisiocampa disstria* and *americana* (imago) are eaten by four kinds of vireos, three kinds of fly-catchers, both cuckoos, robins, rose grosbeaks, scarlet tanagers, cedar wax-wings, catbirds, orioles, red-winged blackbirds, martins, song, chipping, and even English sparrows. I noticed this fact for three successive seasons in

Brandon, Vt., where the pests covered everything. Nuthatches and downy woodpeckers eat them when they find them at rest.

"Chipping sparrows—in my experience—will chase almost any butterfly and often kill kinds they do not seem to eat. I have watched the chase and seen the dead butterflies which fell to the ground. These sparrows seem to enjoy the chase, turning, twisting, tumbling in the air, and I have seen them chase a blowing dead leaf in the same way, following it until it touched the ground.

"I have seen English sparrows catch *P. pandorus* and *achemon* moths, having first hunted them out of a woodbine, bite off the wings and carry the bodies to trees or roofs, presumably for food, though I have not seen the act of eating them. I have not seen this many times."

"Nuthatches, black and white creepers, brown creepers, eat the noctuid moths which hide in crevices of the bark and under the eaves of houses or piazzas, in the blinds or folds of awnings. I have often watched nuthatches go thoroughly over the cornice of our house, dropping one pair of moth wings after another, then go the length of the gutter-pipe on the piazza roof. They are the most methodical and thorough hunters I know among birds except the little summer warbler, which will clear a pea vine of aphids so that not one could I find in a careful search. It cleans one vine before going to another unless startled away. Of course these are only my personal experiences, and I learned years ago that experiences vary much, even with the same species, under different conditions.

"Your paper seems to show a lack of belief in the value of 'imitation' as a protection to butterflies, and rejoices me, for observation compels me to believe that too much value has been placed on this as on the theory that flower colors please insects."

The ornithologists appear to have had the same experience as the entomologists.

Dr. J. A. Allen writes me under date of January 31, 1902: "In regard to birds catching butterflies, I have consulted with Mr. Chapman about the matter, and neither of us recall having seen birds capture butterflies except in rare sporadic instances. It is certainly not a habit of birds to prey upon butterflies."

Dr. S. H. Scudder,[1] in 1870, writes: "Although I have hunted butterflies for fifteen years, I confess I have never seen one in a

[1] *Nature*, iii, 1870, p. 147.

bird's bill, and my faith in that method of lessening their numbers is very slight."

Afterward, in a letter dated October 9, 1901, he says: "I believe that in temperate countries butterflies at least are rarely attacked by birds. I have myself seen proof only once in New England."

Mr. F. P. Drowne informs me that he once saw a phœbe bird catch *Pieris rapæ*, or a similar species, in Virginia.

Mr. William Dearden tells me that he saw a pewee catch a small butterfly, and a kingbird catch *Pieris rapæ*.

In Florida, as we have been informed by Mrs. Annie T. Slosson, the mocking bird frequently chases butterflies, but she has not observed any other bird thus occupied.

In his "Notes on the Food of Birds," 1901, Prof. Cockerell gives no cases of butterflies being pursued and eaten by birds.

Prof. W. M. Wheeler, of Austin, Tex., under date of February 6, 1902, informs me that he has never seen birds pursuing butterflies.

My friend and pupil, Mr. T. E. B. Pope, tells me he once saw an English sparrow pecking away at a *Macrosila 5.-maculata;* he does not know whether it caught it or found it crippled. Another member of my class distinctly remembers seeing a kingbird catch a butterfly; Mr. H. H. Hill, another pupil, saw a kingbird chase and catch "a small white butterfly," and another member of my class, Miss Geraldine E. Street, has seen "a sparrow chase a little white butterfly."

Prof. C. V. Weed, of Durham, N. H., writes that he saw an Antiopa butterfly in the mouth of a Maryland yellow throat.[1]

Prof. E. A. Popenoe, of Manhattan, Kan., under date of February 3, 1902, writes: "I have occasionally seen butterflies chased by birds. So far as I can recall *Pieris rapæ* is the species."

Mr. Wm. T. Davis writes November 4, 1901, that he "observed several English sparrows endeavoring to capture a *Deilephila lineata;* the moth flew in circles, while the sparrows made vain efforts to head it off." It is quite a common thing to see them catch such moths as *Spilosoma virginica*, and also Datana. "My wife saw a bird (species not recognized) catch a little white butterfly, she thinks a cabbage butterfly, in the garden. I have not seen birds catch butterflies, though I have seen great crested fly-catchers and kingbirds catch small moths, etc. I once observed a chipmunk capture a noctuid."

[1] See "*Nature Biographies*," 1903.

"In July, 1897, at Newfoundland, N. J., I saw two specimens of the large dragon fly, *Hagenius brevistylus*, chasing species of Papilio and *Limenitis ursula*. They would station themselves on dead limbs, and when a butterfly came by they would sally forth after the pilgrim like robbers of old from their wayside castle. I did not see them catch any butterflies, though they came pretty near to doing so. Mr. Calvert writes me that Dr. Hagen has a note in *Ent. Monthly Mag.* (1884?) on *Anax longipes* catching Papilio at Wood's Hole.

Among those whose attention I have called to the matter, Prof. James G. Needham, of Lake Forest, Ill., writes that "neither I myself nor any of my students have seen a bird chase and eat a butterfly."

Miss Annie H. Pritchett, of Austin, Tex., and Mr. Ernest Ingersoll write to the same effect.

The late Mr. C. V. Riley states[1]: "Individually I have on several occasions seen butterflies captured by birds, and have seen dragon flies dart after them." He adds that "any amount of evidence might be collected on this head," but we are convinced that this is an over-statement.

3. The Case of the Milkweed Butterfly (Anosia plexippus).

It is a generally accepted belief, first expressed by Walsh and Riley in June, 1869,[2] that this butterfly enjoys an immunity from the attacks of birds by reason of its nauseous taste or odor, and that *Basilarchia archippus* (*disippus*), which is edible and inodorous, is protected by its resemblance to its model. This hypothesis has been generally accepted, and yet it needs far more facts of observation to support it than have yet been brought forward. Just how nauseous or malodorous Anosia is needs further investigation.

We have been able to find in the literature but two cases of the Anosia being caught by birds, while there is no record, says Riley, "of any person having actually seen a bird or other animal attack the species of Limenitis in this country," Limenitis being a synonym of Basilarchia, the mimic.

The first case is recorded by Riley,[3] who relates an occurrence noticed by the late Mr. Otto Lugger, then of Chicago. "While

[1] *Third Ann. Rep. Insects Missouri*, 1871, p. 167.

[2] *American Entomologist*, I, June, 1869, p. 189.

[3] *Third Annual Report Insects Missouri* 1871, p. 169. Footnote 1.

employed on the U. S. Lake Survey he once saw a bird dart after an Archippus butterfly, seize it and immediately drop it without devouring the body. The butterfly dropped close by his side and he picked it up and examined it, and had no means of accounting for the singular action of the bird."

The second case is thus mentioned by Mrs. Mary Treat:

"The beautiful Archippus butterfly, *Danais archippus*, is a common species and enjoys a wide range. It occurs in Upper Canada and extends into South America, where, according to Prof. Agassiz, it is common throughout the region of the Lower Amazon, and in the Mississippi Valley it is one of the most frequent species. This Archippus butterfly enjoys almost perfect immunity from enemies. Neither birds nor any of the hymenopterous parasites will interfere with it. It probably has a nauseous, disagreeable taste that birds do not relish. Last summer a pair of kingbirds built their nest on a low limb of a tree close to our door. . They consumed and fed to their young a great many butterflies, especially the Rape butterfly. Toward evening they were very active, taking indiscriminately all insects that ventured on the wing—great grasshoppers and cicadas, as well as butterflies. One evening several Archippus butterflies came to their tree as they were fluttering about fixing themselves on the branches for the night; the kingbird very comically turned his head from side to side, eyeing them closely; becoming satisfied with his observations he gave his head a sudden jerk and vigorously wiped his bill on the limb, as if the remembrance of the disagreeable morsel was enough to nauseate him."[1]

The Heliconidæ are said by Bates to have a peculiar smell. According to Wallace (*Contributions*, etc., p. 78), when an entomologist "squeezes the breast of one of them between his fingers to kill it, a yellow liquid exudes which stains the skin, and the smell of which can only be got rid of by time and repeated washings." Messrs. Walsh and Riley in their joint article on Anosia state: "We ourselves have never noticed any particular smell about it, but we can add our testimony to the negative fact of its never being attacked by any carnivorous animal, so far as our experience has gone" (*Amer. Ent.*, I, p. 187). The nauseous secretion probably emanates from the scales, as Burgess in his anatomy of the milk-

[1] From "Butterflies and Moths," by Mary Treat, in *Hearth and Home*, Vol. 4, Jan. 13, 1872, p. 25.

weed butterfly does not mention the occurrence of any anal or other fœtid glands.

The only case mentioned by Belt in *The Naturalist in Nicaragua* is the following: "Thus I had an opportunity of proving in Brazil that some birds, if not all, reject the Heliconii butterflies, which are closely resembled by butterflies of other families and by moths. I observed a pair of birds that were bringing butterflies and dragon flies to their young, and although the Heliconii swarmed in the neighborhood and are of weak flight so as to be easily caught, the birds never brought one to their nest." He mentions no case of birds eating butterflies in Nicaragua, though a tame white-faced monkey would greedily eat butterflies.

Scudder[1] says that Riley in a letter remarks that the butterfly "has a rank but not strong smell," and Scudder adds: "Experiment shows that all the scales have a carroty odor, and that those in the pouch of the hind wings differ from them only in being stronger scented with a slightly honeyed character."

According to an early statement by Scudder,[2] the eggs and larva of Anosia enjoy a greater immunity from the attacks of parasites than those of other butterflies. From this Mr. Wallace[3] infers that the peculiar secretions of the butterfly "extend to their larva and egg state"; but this statement concerning parasites, repeated in his later work, entitled *Darwinism*, appears to be an assumption not based on rigid investigation, for Dr. Scudder in 1889[4] corrects his earlier statement and says that Anosia has its fair share of parasites, *i.e.*, not only an egg-parasite but an ichneumon and Tachina parasite of the larva, while from a single pupa issued over fifty Pteromalus flies.

Here it might be added that Seitz[5] questions whether the Heliconidæ are themselves invariably malodorous, denying that this is invariably the case. He tested as many as fifty species of Danaids, both African and American, but could not recognize the least odor, disagreeable or otherwise; and a number of these species were models for mimicry. In some but not in all Heliconids, Dr. Seitz

[1] *Butterflies of New England*, I, p. 745.

[2] *Nature*, III, 1870, p. 147.

[3] *Nature*, III, Dec. 29, 1870, p. 165. Also see *Darwinism*, 1889, p. 238.

[4] *Butterflies of New England*, I, p. 745.

[5] *Zool. Jahrbücher Spengel*, III, p. 888. See also Beddard's *Animal Coloration*, p. 197.

detected an odor like that of napthaline. "In *Heliconius beskii*, a species with a particularly evil odor, it was found that only a few individuals were odoriferous . . . the odor is not persistent, but depends upon some variable circumstance, as food."[1]

I may add my own slight experience with *Anosia plexippus*, taken from my notes. September 4 I caught one, and pinching it between my fingers I could not detect any odor, nor could three other members of my family, but Prof. H. H. Wilder detected a slight odor which he compared to that of the larva of *Samia ceceopia*, only the odor of the latter "is ten times as strong." On cutting out a bit of the under side of the middle of the abdomen I tasted it and perceived a very slight taste not like any substance known to me, and certainly not resembling that of laudanum. On removing a larger piece and pressing the abdomen the odor became more distinct, and one of my family at once detected it, although at first before it was wounded she could perceive no odor. I tasted two pieces cut from the middle of the abdomen, but the taste was hardly perceptible and not unpleasant, neither bitter, acid, or in any way pungent.

To sum up, the following birds in the United States of North America have been seen to pursue butterflies, viz.: the black-throated green wood warbler, English sparrow, chipping sparrow, Savannah and song sparrow, thistle finch, kingbird, phœbe bird, pewee, mocking bird, purple martin, scarlet tanager, crow blackbird, cuckoo and shrike.

Butterflies of the following species have been actually seen to have been eaten: *Pieris rapæ* (many more than any other kinds), *Vanessa milberti*, *Brenthis myrina*, while *Papilio turnus* and *P. cybele* were not eaten. It is evident that for temperate North America and for Europe the evidence is entirely too slight to even suggest the theory.

4. Facts in Favor of the Bates-Müller Hypotheses.

The strongest body of facts in favor of the view that birds in confinement have an appetite for butterflies is afforded by Mr. F. Finn in his "Contributions to the Theory of Warning Colors and Mimicry,"[2] his observations having been made in India. He concludes that there is a general appetite for butterflies among insectivorous birds, "even though they are rarely seen when wild to

[1] Quoted by Beddard, *l. c.*, p. 197.

[2] *Journal of the Asiatic Society of Bengal*, LXVII, 1897, pp. 613–668.

attack them." His experiments were made with caged passerine birds of the babbler and bulbul groups.' He fed the birds with a number of non-warningly-colored butterflies, together with four *Danais chrysippus* and a Delias. On five occasions the supposed inedible Danais was eaten by the bird, and at other times the Danais were eaten, though on the whole the edible species were preferred by the Liothrix, while Mr. Finn was not so sure about the bulbuls. In other series of experiments the "protected" butterflies were eaten by the bulbuls, even when offered as a choice a non-protected Catopsilia.

It is to be observed that the birds would peck at Euplœa and other protected butterflies, and afterward wipe their beaks, but subsequently would return to the attack, beat off the Euplœa's wings and swallow it. It thus seems that even if a bird wipes its beak as if in disgust after attacking an inedible butterfly, it may eventually devour it.

Experimenting with a single bird in a cage, the racket-tailed drongo shrike, it eat "without persuasion" several *Danais chrysippus* and three *D. genutia*, and "with persuasion" two *Papilio aristolochiæ* and a *P. polites*, though maggots had been fed to them or were available. The foregoing experiments give us the impression that these birds in nature would not eat butterflies, when seed, fruit or maggots, etc., were to be had.

Experimenting with birds at liberty, on giving a *Papilio demoleus* to a wild mynah (*Acridotheres tristis*) which he had seen trying to get at some butterflies in an insect cage, the bird knocked off most part of the butterfly's wings and flew off with the body. Another mynah seized a disabled *Danais genutia*, and after battering it ate most of it. Another mynah seized a disabled Catopsilia and *Danais limniace*, knocked off a fore wing of each and flew with them to a high building. On another occasion birds of the same species pecked at Papilios, then leaving them.

Of two hornbills (Anthracoceros) one did not care about insects at all, while the other readily ate several unprotected butterflies, but "took, rubbed and refused *Danais chrysippus* and *D. genutia* and Euplœa," yet it also refused a Junonia and a Papilio.

It seems, then, in the words of Mr. Finn, that the common babblers (*Crateropus canorus*) ate the Danaid butterflies readily enough in the absence of others, but when offered a choice showed their dislike of these "protected" forms by avoiding them. "This

avoidance was much more marked when the birds were at liberty, though even so a few of the objectionable butterflies were eaten." He saw a wild red-vented bulbul eat a white butterfly.

"Although I did not experiment on any of these at liberty, my experience with the Liothrix (*Liothrix luteus*), mesia (*Mesia argentauris*), bhimraj (*Dissemurus paradiseus*), king crow (*Dicrurus ater*), starling (*Sturnus menzbieri*), and shama (*Kittacincla macrura*) was similar in that all of these birds objected to the Danainæ, *Delias eucharis* and *Papilio aristolochiæ*, especially, as a rule, to the last, in comparison with other butterflies, or absolutely."

"I never *saw* the Chloropsis (*Chloropsis aurifrons* or *malabarica*) or the Sibia (*Malacias capistrata*) eat any 'nauseous' butterfly, except that in the case of the former one Euplœa body and a few bits of wing were eaten."

"The latter bird refused with apparent dislike the male of *Elymnias undularis*, which should be palatable, and was as a matter of fact usually liked by the birds to which I offered it. Another mimetic species, *Papilio polites*, was not very generally popular with birds, but much preferred to its model, *P. aristolochiæ*."

"In several cases I saw the birds apparently deceived by mimicking butterflies. The common babbler was deceived by *Nephronia hippia*, and Liothrix by *Hypolimnas misippus*. The latter bird saw through the disguise of the mimetic *Papilio polites*, which however was sufficient to deceive the bhimraj and king crow."

"Young hand-reared birds, like the shama and bhimraj, had no instinctive knowledge of the 'nauseous' forms, and ate them quite readily at first, but soon gained experience. Birds caught when old, when watched from the first, like the Sibia, first Mesia and starling, appeared to know and avoid unpalatable species."

He finally concludes: "That many, probably most species dislike, if not intensely, at any rate in comparison with other butterflies, the 'warningly-colored' Danainæ, *Acræa violæ*, *Delias eucharis*, and *Papilio aristolochiæ;* of these the last being the most distasteful, and the Danainæ the least so."

5. Adverse Evidence, from Observations Made in Europe and Asia.

Prof. Theo. D. A. Cockerell writes: "When I was a boy in Sussex, England, there was a wooden summer house roofed, but

open at the sides, in which we used to find great quantities of moth's wings. The wings were scattered over the floor, and were mostly of noctuids; the only species I now recall definitely is *Scoliopteryx libatrix*. We always supposed that this destruction was the work of bats, but now I think of it, we had no real proof of that."

R. Newstead, in the *Gardener's Chronicle*, 1901, pp. 197, 217, states that a fly-catcher (*Muscicapa grisola* L.) was seen flying after butterflies, but each time when it could seize it stopped and let the butterfly escape.

Mr. A. G. Butler[1] states: "I have collected in Kent for at least thirty years, and it must be quite twenty-five years since I last saw *Aporia cratægi* flying in that county, but during the whole of the thirty years I have never seen any bird but a sparrow attempt to catch a butterfly."

Previously,[2] however, he says: "I have frequently seen birds catch and devour the unprotected species upon the wing."

Prof. L. Katharina[3] had an opportunity to observe a striking case of the chase and capture of butterflies by a bird. "I was with Dr. Escherich in Central Asia, May 6, 1895, where I was busy in a fallow field in the neighborhood of Angora catching *Thais cerysii*, which at this time flew in such numbers that I could catch six at a time in my net, when a flock of bee-eaters (*Merops apiastor*) began to attack them. I heard the snapping of their bills and in a very short time there was no trace of the slowly flying butterflies left, and the birds disappeared." He had at home seen the redstart (Ruticilla), which has a special predilection for butterflies, seize flying Pieris and carry them to their nests. "An ornithological friend tells me that he has often raised caterpillars so as to feed the butterflies to his birds, and that the chaffinch (*Fringilla cælebs*) are great lovers of them."

"I am convinced that the very beautiful protective coloring of butterflies is of no use, the bee-eater being attracted by their fluttering motion. I also think that the mimicry of protected species by those not protected (Danaidæ, Papilionidæ, etc.) has as regards color and markings no great value.

[1] *Entomologist's Monthly Magazine*, London, XXIV, p. 40, July, 1887.

[2] *Nature*, III, p. 165.

[3] "Werden die fliegenden Schmetterlinge von Vögeln verfolgt?" *Biol. Centralblatt*, 1898, p. 680.

"When a deception of its enemy by a flying butterfly occurs this happens mostly through the mimicry of the mode of flight of the protected butterfly."

"The experienced collector to some extent recognizes a species by its flight, and is unable to recognize it by its color and marking on account of the distance and rapidity of its flight, or for some other reason. I say intentionally the species, since the species of one and the same genus is distinguished from one another by certain peculiarities of flight, or by its appearance when at rest, etc.

"But what attracts the eye of the collector may certainly more readily attract the notice of animals engaged in the pursuit of butterflies. I should only consider such cases of mimicry as protective mimicry in which the model, besides form and size, also mimics it *in the peculiarities of its movements*. Isolated statements thereupon are scattered through the literature, but so sparsely that most of the cases regarded as those of mimicry should most of them be considered as cases of similarity of development resulting from similar external conditions, above all climatic; certainly not to selection."

Dr. Carl Russ expressly recommends seeking for butterflies as a special dainty for singing birds.

In an article on the pursuit of butterflies by birds, called out by that of Prof. Katharina, Prof. J. Kennel,[1] of Dorpat, states that a pair of warblers (Sylvia) fed their five young all day long with *Vanessa urticæ*, some *Parnassius ammemosyne* and *apollo*, which last species was very rare in that region (the Estland coast), also *Pieris rapæ*, and on many days Libellulidæ. The butterflies were carried to the nest with their wings "cut in pieces." Also among the woods were scattered the wings of different species of Catocala, Arctia, Euprepia, whose bodies may have been eaten by bats and the goatsucker (Caprimulge), or perhaps by small owls.

"Near Kreman, Liveland, I found one day among the bushes a freshly emerged *Pleuretes matronula* and nearby the wings of two other specimens. Here was proof that these Lepidoptera were caught by birds (or bats) and eaten, all except the wings." He also had seen swallows catch small moths (*Tortrix viridana*) and small Noctuina.

He concludes that (1) such butterflies as are caught by birds are edible, and (2) that their colors are neither protective or warning to the pursuer.

[1] *Biol. Centralblatt*, 1898, pp. 810–812.

"Notwithstanding that insect-eating birds are relatively rare, and perhaps only exceptionally capture butterflies, the latter are with their small bodies and large wings difficult to seize. As a rule only such birds as swallows with their long bills can catch them. And because of this difficulty in butterflies their colors and markings are not of very much importance. They are all rejected or captured exceptionally, but at the same time almost without choice.

"It is not to be denied that many species are perhaps truly inedible, but this must be carefully confirmed by painstaking observation. It seems inadvisable to draw conclusions as to inedibility and protection only from coloring, markings, shape of wing, or special odors, which are not essentially perceptible to us."

Weismann, in his *Vorträge*, etc. (1902), claims that many butterflies are sacrificed by birds, though he records no instance of his own observations, but quotes Pöppig as saying that in the primitive forest of South America it is not difficult to recognize where one of the Galbulidæ has chosen its favorite perch, since the wings of the largest and most splendid butterflies, whose bodies are alone eaten, cover the ground for some steps in circumference.

Direct observations on the pursuit of butterflies by birds are due especially to Dr. Hahnel, who while collecting in Central and South America found many opportunities of observing it. He writes: "No other kind of butterflies are so much hunted as the Pieridæ, and these robbers often snapped up the most beautiful and fresh specimens close to me. The unfailing certainty of their flight made me wonder, and I willingly paid for the spectacle with the loss of a specimen." As to the chase of that large species of Caligo, on whose leaf-like under side is an ocellus, he says: With incredible adroitness did the great creature escape the strokes of the beak of the bird following hard after it and escape from one bush to another, until finally the hunted game was driven into the thickest of the mass of tangled branches and the tired bird flew off to a distance on another chase. Hahnel adds that the wonderfully beautiful *Morpho cissus* was seized by dragon flies, while quantities of lizards pursue and eat butterflies (Weismann). Caspari observes that swallows catch butterflies. He once let about a hundred *Vanessa antiopa* fly out of his window, "but scarcely ten reached the woods nearby, the rest were eaten by the swallows," which collected expressly for the purpose before his window.

Slevogt has brought forward many proofs that our native butter-

flies suffer much harm from birds, though Weismann does not quote his instances.

But another German naturalist, Eimer, had previously arrived at a different conclusion. In his *Ontogenesis der Schmetterlinge* he remarks: "But who has ever seen a bird flying after butterflies to such an extent that by this means a protective transformation through selection could be attained?" From his own experience Eimer only remembered one case, *i.e.*, where a redstart (*Ruticillus phœnicurva*) seemed to carry a Pieris (?) in its beak. From lepidopterists and his students he could only get information regarding scattered cases where butterflies were pursued by birds.

Cases observed in India and Ceylon.—About the year 1884 a discussion arose in the Bombay papers as to whether birds preyed on butterflies, and the general opinion expressed was that it was comparatively rare for them to do so. This led Col. Yerbury to notice such occurrences, with the following results. He saw a young king crow (*Dicrurus ater*) stoop at a big blue Papilio and miss it. The bird did not repeat the attempt. He afterward saw a young king crow stoop at a *Vanessa kaschmirensis*, and after missing it once take it at the second attempt. He did not notice whether the insect was eaten. He saw a bee-eater (*Merops philippinus*) keep flying in front of his carriage and taking Pierinæ as they rose in clouds. The bird seemed to select the yellow females, which are rare, the white females being to them probably in the proportion of 100 to 1. "An ashy swallow shrike (*Artamus fuscus*) caught six Euplœa (*Crastia cove*)." (Marshall and Poulton.)

Cases observed in Burmah.—Col. Bingham saw a bee-eater (*Merops swinhoei*) catch a butterfly (Cyrestis); more than once it missed a butterfly, but eventually caught it; of the butterflies hawked and eaten by the bee-eaters there were five species. "I also particularly noticed that the birds never went for a Danais or Euplœa or for *Papilio macareus* and *P. xenocles*, which are mimics of Danais, though two or three species of Danais, four or five of Euplœa, and the two above mentioned mimicking Papilios simply swarmed along the whole road." The large *Merops philippinus* with some king crows were seen hawking Catopsilia, flying in clouds. The pigmy hawk or falconet (*Microhierax cœrulescens*) was seen seizing a *Papilio sarpedon* in his claws. This bird also uses butterflies' wings to form a pad for the bottom of its nest made in a hole of a dry tree.

Mr. A. G. Butler[1] states that an entomologist in Bombay had informed him "that the *Charaxes psaphon* of Westwood was continually persecuted by the bulbul, so that he rarely captured a specimen of this species which had not a piece snipped out of the hind wing; he offered one to a bulbul in a cage, and it was greedily devoured, whilst it was only by repeated persecution that he succeeded in inducing the bird to touch a Danais, which he offered to it."

In his article "Mimetisme," Piepers refers to his experience during twenty-nine years spent in Java.

"One day when a *Euplæa rafflesii* Moore, *i.e.*, a Danaid reputed to be inedible, was disclosed in my garden where several of the caterpillars of this species had lived, I saw a bird (Edolius?) seize and eat it; the next day another shared the same fate. Twice also have I seen a sparrow attack an *Amathusia phidippus* L." These large butterflies, though Rhopalocera, only fly at twilight, and the one attacked had taken refuge on a whitewashed wall. "These four cases are the only ones during the twenty-eight years of my sojourn in the Indies where I have seen birds attack any butterflies. And even to justify the fact in question it is not enough that here and there a butterfly is eaten by birds, but there should be a chase of this kind so general and common that the existence of unprotected species should be endangered, and that an evolution like their assumed mimicry should become of great utility. Moreover the same thing occurs in other regions. Pryer has never seen an instance during twenty years entomologizing in Borneo, nor Skertchley during thirty years of observation in Europe, in Asia, in Africa and in America. According to this last the celebrated entomologist Scudder would not credit this fact. In the session of the London Society named below, held May 3, 1869, Home enumerated a number of insects which he had seen in India devoured by several kinds of animals; among these insects he mentioned moths but no butterflies. Here in Holland it is also the same thing. According to observations published in 1890 by Butler, a small English bird, also found with us in captivity, devoured with apparent relish hundreds of *Pieris brassicæ* and *P. napi*, but it is not observed here that the birds chase these butterflies, although they are very common. Moreover as to England, Jordan has at times seen a certain small insectivorous bird seize a butterfly, but Butler states that

[1] *Nature*, III, p. 165.

during thirty years' residence in Kent he has not observed a single fact of this kind.

Mr. Skertchly's statement is as follows:

"Mr. W. B. Pryer, in his notes on the Rhopalocera of British North Borneo, casts a doubt on certain points connected with the theory of mimicry, stating that during twenty years' collecting in the Far East he never saw a butterfly taken by a bird.[1] Discussing this question with him in England and Borneo I was led to study the matter more particularly, and as my work takes me for months at a time into the virgin forest, my opportunities have been unusually great. . . . . That mimicry does exist probably no one has ever doubted since Bates first called attention to the phenomena. The explanation, too, proffered at the time, that edible species copied nauseous morsels, was so simple, so full, so entirely explanatory that, like Darwin's theory of coral reefs, it seemed unassailable. Indeed so strong was this feeling, that few naturalists ever seem to have looked for facts to support it.

"Yet how meagre the evidence is! Surely if birds are in the habit of eating butterflies as a staple article of food, the fact would be patent to every ornithologist and entomologist, to every one who delights in the beauties of nature. Such is not the case, and even Distant, in his 'Rhopalocera malayana,' can only cite a few isolated cases. That some birds frequently, and others occasionally, devour butterflies is certain. But these are rare exceptions.

"Mr. Pryer's remark has been paralleled by Mr. Scudder, and after thirty years' observation of insects and birds in Europe, Asia, Africa and America, I can confidently assert that I have never yet seen a bird take a butterfly."[2]

Prof. E. A. Minchin, while in Madras, saw a bird swoop down and carry off a butterfly (*Elymnias undularis*).[3]

6. Cases Observed in Natal, South Africa.

In his "Five years of observations and experiments on the bionomics of South African insects," G. A. K. Marshall gives records

[1] *Annals and Mag. Nat. Hist.*, Jan., 1887, p. 44. Mr. Pryer's statement is as follows: "Moths are ruthlessly eaten by birds by day and by bats at night; but I have never once in a twenty years' experience seen a butterfly taken by a bird." (A. S. P.)

[2] *Annals and Mag. Nat. Hist.*, 6th Ser., III, 1889, p. 477.

[3] *Trans. Ent. Society, London*, 1904, p. xxxvii.

of attacks on butterflies by wild South African birds. He remarks: "Personally I do not suppose I have seen such an occurrence more than perhaps half a dozen times, the birds being the paradise fly-catcher (*Terpsiphone perspicillata*), the bee-eater (*Merops apiaster*), and two rollers (*Coracias spatulata* and *Eurystomus afer*); but then I admit that I have paid little or no attention to the matter until quite recently." This was in a letter written in Natal, October 7, 1897. After this, as Prof. Poulton states, Mr. Marshall kept a careful record of his observations. At Durban he saw a paradise fly-catcher catch a specimen of *Eronia cleodora*, seizing it *with its feet*, and carry it off. In 1898 he saw a Marico wood shrike (*Bradyornis mariquensis*) dart down from a tree and catch a *Sarangesa eliminata* (Holl.) which was sitting with outspread wings on a small plant. He saw a bush kingfisher (*Halcyon chelicutensis*) catch and eat two butterflies (*Junonia cebrene* and *Catopsilia florella*), both of which were captured when feeding. He also saw a fly-catcher (*Pachyprora molitor*) make several futile attempts to catch a *Tarucus plinius*. A drongo (*Buchanga assimilis*) was seen flying past with a white butterfly (probably *C. florella*) in its beak. Remains of a *Papilio demodocus* were found in the stomach of a cuckoo (*Coccyster caffer*).

In 1899 a paradise fly-catcher passed by and with a loud snap of its beak tried to catch a butterfly (*Atella phalantha*), which escaped, though the bird had cut off the tip of one wing. A hobby (*Falco subbuteo*) had in its stomach an almost entire Terias. He saw a drongo catch a white moth, and almost at once drop another white moth of the distasteful genus *Diacrisia* (*D. maculosa*). An observer at Gazaland saw a South African stonechat (*Pratincola torquata*) in chase of a *Tarucus plinius*, and he saw the wings of a lot of butterflies (chiefly *P. corinneus*) below the branch of a tree on which some swallows were constantly settling. Marshall saw a drongo hawking insects from the top of a dead tree. "There were many *Pierinæ* about, chiefly Teracolus and Belenois, but the bird paid not the least attention to them." At last one with broken wings went by so that its flight was weak and erratic; the drongo swooped down on it, but the butterfly dropped into the long grass. "This episode would point to the conclusion that the fact that birds refrain from pursuing butterflies may be due rather to the difficulty in catching them, than to any widespread distastefulness on the part of these insects."

The beautiful plates illustrating the injuries to the wings of various butterflies attributed to the bites of birds, lizards, etc., are of much interest, though even if it were proved that the mutilations were actually due to the attempts of such vertebrates to seize the insects, rather than to their being battered and torn by wind or rain, they scarcely form a body of evidence proving that butterflies constitute an important article of food for birds, but rather that they are only stray tid-bits; much less does the evidence seem to us sufficient to afford a foundation for a theory of the origination of species.

Thus of the twenty-five figures on Pl. IX, it is stated that ten of the figures reprcsent mutilations attributed to the bites of lizards, and one to the attacks of a mantis. Of the thirty-three figures on Pl. X eleven are referred to the attacks of birds, six to those of lizards, while the others are not explained. Of the twenty-four figures on Pl. XI thirteen are referred to the bites of birds, one to the attempt on the part of a lizard and two to injury by a possible mantis.

Mr. Mansel Weale[1] mentions seeing in Brooklyn, Kaffraria, *Tchitrea cristata* darting at *P. agathina;* "*Cypselus caffer* I have seen take small moths from the grass, and dart at *Terias rahel* on our open flats; *Motacilla capensis* I have seen take moths and *P. hellica; Dururus musicus* is a voracious bird amongst insects, and takes moths, though I cannot state I have seen it capture Rhopalocera, yet I think it also attacks Pieridæ."

7. The Bates-Müller Theories.

The theory of protective coloration, *i.e.*, that animals of many groups are protected from observation by their color, is generally accepted, though there is a difference of opinion as to the active cause of the adaptation, or harmony, *i.e.*, whether it is the result of the physical agency of light and shade, with or without moisture, or is due to natural selection.

The Batesian theory.—Mr. Bates[2] first states that the majority of the species of Heliconidæ have very limited ranges. "I was surprised," he says, "when traveling on the upper Amazons from east to west, to find the greater part of the species of Ithomiæ changed

[1] *Nature*, III, p. 508.

[2] *Trans. Linn. Soc. London*, xxiii, 1862, pp. 495–566.

from one locality to another, not further removed than 100 to 200 miles. . . . . This is remarkable when we consider that the whole of the country of the upper Amazons is a nearly level plain, uniformly covered with forest, and offering no perceptible difference in soil or other physical conditions." Many of these local species have the appearance of being geographical varieties, but they are "good and true species"; where a number of very closely allied species fly together they keep themselves perfectly distinct, not hybridizing. These species led Bates to believe that "many of the now distinct species of Heliconidæ have arisen from local varieties, segregated from the variations of preëxisting widely disseminated species." Corresponding races of counterfeiting butterflies of other families and moths accompany these local forms. "In some places I found proof that such species are modified from place to place to suit the peculiar forms of Heliconidæ there stationed." He then mentions the well-known case of the mimicry of Ithomia by Leptalis. The Ithomiæ are all excessively numerous in individuals, while the Leptalides are exceedingly rare, and "cannot be more than as 1 to 1000 with regard to the Ithomiæ." In a polymorphic form like the *Leptalis lysinæ*, the variations he thinks "have not arisen by simple variation or *sports* in one generation, but, as we shall presently see, by an external agency accumulating the modifications of many generations, in two diverging directions." On p. 508 he states that it is "clear that the mutual resemblance in this and other cases cannot be entirely due to similarity of habits or the coincident adaptation of the two analogues to similar physical conditions," yet in the next sentence he remarks: "I think the facts of similar variation in two already nearly allied forms do sometimes show that they have been affected in a similar way by physical conditions," adding that a "great number of insects are modified in one direction by a seaside habitat." "I found also the general colors of many widely different species affected in a uniform way in the interior of the South American continent. But this does not produce the specific imitation of one species by another; *it only prepares the way for it.*" The italics are ours, and in this pregnant sentence we have the whole matter of mimicry in a nutshell. The physical agents, variations of light and heat, are what prepare the way; they are the initial causes.

Bates then asks what advantage the Heliconidæ possess to make so flourishing a group, adding: "It is probable they are unpalatable

to insect enemies." And then after stating that they all have a peculiar smell, he mentions almost incidentally: "I never saw the flocks of slowly-flying Heliconidæ in the woods persecuted by birds or dragon flies, to which they would have been an easy prey; nor, when at rest on leaves, did they appear to be molested by lizards or the predaceous flies of the family Asilidæ, which were very often seen pouncing on butterflies of other families." Here it may be added that Bates nowhere states that he ever saw a bird pursuing or devouring a butterfly, and does not dwell on this subject, beyond remarking (on p. 499) that the Heliconidæ "show every sign of flourishing existence, although of slow flight, feeble structure, unfurnished with apparent means of defense, and living in places which are incessantly haunted by swarms of insectivorous birds."

Bates' explanation of the origin of mimetic species is by natural selection, although he says: "In what way our Leptalis originally acquired the general form and colors of Ithomiæ I must leave undiscussed." He suggests, however (p. 512), that the selecting agents are insectivorous animals, which gradually destroy those sports or varieties that are not sufficiently like Ithomiæ to deceive them." He also says: "The conditions of life of these creatures are different in each locality where one or more separate local forms prevail, and those conditions are the selecting agents."

Bates' discussion of this subject is broad and sound, due to his observations over wide regions of country, and to careful studies on his return to England. He was evidently impressed with the fact that local varieties arise from local conditions of the environment, and does not entirely rely on the attacks of insectivorous birds; in this respect he is less narrow than later writers on mimicry, allowing as he does, and even seeming to waver between, the modifications due to changes in the physical conditions and the action of insectivorous birds alone.

How Mr. Bates regarded the subject seventeen years later may be seen by his comments on Müller's theory, made at a meeting of the Entomological Society of London in June, 1879 (*Trans.*, p. xxviii), which we quote on p. 419.

Here might be cited the statement of another naturalist, Dr. Seitz,[1] who found in a forest of southern Brazil a perfectly circumscribed region in which the insects were almost entirely blue; a few

[1] *Zoolog. Jahrbücher*, V, p. 317, 1890. Quoted by Beddard, "Animal Coloration," p. 46.

miles away from this locality the insects were red, yellow—any color but blue; but in this particular locality blue was so characteristic a tint, that out of twenty butterflies ten were entirely blue and the remaining ten partially blue. Nor was blue found to be confined to the Lepidoptera, the flies and Hemiptera were also largely blue. Dr. Seitz adds that we must not put down every color to mimicry, need for protective resemblance, warning coloration and so forth; for there are plenty of phenomena which do not seem capable of explanation on any of these theories.

Müller's theory.—In his paper published in *Kosmos*, May, 1879, and translated with notes by Mr. Meldola in the *Transactions* of the Entomological Society of London, for the same year, Müller stated his theory.

After discussing the resemblances in shape and color between *Ituna ilione* and *Thyridia megisto*, and the structural differences which prove that they must have had separate ancestors, he inquires which is the original form and which the mimic. "Does not," he says, "a species which serves as a model occur always in countless swarms, while the mimic is a hundred times more rare? Does not the model bear the hereditary coloring of its genus and family, while the mimic appears in borrowed plumes? And finally, is not the model unpalatable on account of its repulsive taste and odor, being for these reasons safe from foes, while the mimic finds protection in its disguise, without which it would be devoured as a tasty model?"

Müller then states that the imitating species may, at least in some districts, be more common than its model; "it is also conceivable," he says, "that the model species may become extinct while the mimicking species remains unaffected." He then says that in the case of the Ituna and Thyridia under consideration, both species are rare, at least in Santa Catharina, "and their relative numbers give no clue, therefore, as to which is the model." Both also are equally well protected by distastefulness. He also adds: "Now what does the mimicry of protected species signify? What advantage can it be to the rare *Eueides parana* to be so wonderfully like the common *Acræa thalia*, and what benefit can one species derive from resembling another, if each is protected by distastefulness? Obviously none at all if insectivorous birds, lizards, etc., have acquired by inheritance a knowledge of the species which are tasteful or distasteful to them—if an unconscious intelligence tells them

what they can safely devour and what they must avoid. But if each single bird has to learn this distinction by experience, a certain number of distasteful butterflies must also fall victims to the inexperience of the young enemies. Now if two distasteful species are sufficiently alike to be mistaken for one another, the experience acquired at the expense of one of them will likewise benefit the other; both species together will only have to contribute the same number of victims which each of them would have to furnish if they were different. If both species are equally common, then both will derive the same benefit from their resemblance—each will save half the number of victims which it has to furnish to the inexperience of its foes. But if one species is commoner than the other, then the benefit is unequally divided, and the proportional advantage for each of the two species which arises from their resemblance is *as the square* of their relative numbers.

"If two species are concerned, of which the one is very common and the other very rare, then the advantage falls almost entirely on the rarer species. If, for example, *Acræa thalia* were a thousand times commoner than *Eueides parana*, the latter would derive a million times greater benefit from the resemblance of the two species, whilst for the Acræa the benefit is practically *nil*. Thus *Eueides parana* might by natural selection be converted into one of the most exact mimics of *Acræa thalia*, although it is just as distasteful as the species imitated.

"On the other hand, if two or even several distasteful species are about equally common, resemblance brings them a nearly equal advantage, and each step which the other takes in this direction is preserved by natural selection—they would always meet each other numerically—so that finally one would not be able to say which of them has served as the model for the others. In this manner are explained those cases where several allied distasteful species (*e.g.*, *Colænis julia*, *Eueides aliphera*, and *Dione juno*) resemble one another—cases where such resemblance cannot be regarded as inherited, and yet where neither of the species appear to claim to have served as a model for the others.

"To this category Ituna and Thyridia may belong, although the first has probably made the greater step in passing from the former dissimilarity to the present resemblance of the two species."

It will be interesting to read the comments on this paper made by Mr. Bates at the same meeting. He remarked that "he could

not see that Dr. Müller's explanations and calculations cleared up all the difficulties. The numerous cases where species which are themselves apparently protected by their offensive secretions evidently mimic other species similarly protected still form a great stumbling block. The excessive complexity of the question must be evident to all who read Dr. Fritz Müller's writings on this subject. The phenomena with regard to the Heliconidæ, stated broadly, were these: In tropical South America a numerous series of gayly-colored butterflies and moths, of very different families, which occur in abundance in almost every locality a naturalist may visit, are found all to change their hues and markings together, as if by the touch of an enchanter's wand, at every few hundred miles, the distances being shorter near the eastern slopes of the Andes than nearer the Atlantic. So close is the accord of some half a dozen species (of widely different genera) in each change that he (Mr. Bates) had seen them in large collections classed and named respectively as one species. Such a phenomenon was calculated to excite the interest of the traveling naturalist in the highest degree. Although the accordant changes were generally complete, cases occurred in which intermediate varieties were still extant, and the study of these had given him, when he was in South America, the clue to an explanation which, however, does not embrace the whole of the problem" (p. xxix).

From the facts regarding these local varieties thus stated by Bates, we seem warranted in ascribing the mimetic resemblances to convergence, or exposure to the same conditions of light, heat, moisture, etc., affecting all the individuals of a variety simultaneously, rather than to what is vaguely called "natural selection." A geographical series of each locality arranged in order from east to west would graphically elucidate the problem.

8. Criticisms of the Bates-Müller Hypotheses.

The color and markings of animals in general are primarily due to the action of light and the color of the environment or background. To suppose that in the case of butterflies alone the colors of the mimics are due to the attacks of birds, whereas remarkably few butterflies, as we have seen, are ever eaten by them, is a cause so inadequate, so limited in its scope and so one-sided, that it is no wonder the hypotheses has many opponents.

Mimicry not primarily due to natural selection.—As has been often stated by Semper and others, natural selection is not a transforming agent, but rather results in the preservation of species. With little doubt models and mimics resemble each other because the light and background or environment are the same, and act on great numbers of individuals in a given area.

While Bates, and apparently Fritz Müller, put forward their views in a tentative way, later writers of the extreme Darwinian school, notably Wallace, Poulton, Weismann, and a few others, strongly insist on the entire sufficiency of the selection hypothesis, claiming that it is the sole, primitive cause of the mimicry. Thus Prof. Poulton[1] goes so far as to claim that "birds are among the chief enemies of butterflies," adding: "That they have been the chief, if not the only, agents in the production of mimicry, whether Batesian or Müllerian, "I have little doubt." Again he says: "The intensely procryptic habits and colors of many nymphaline genera have certainly been brought about by selection, due to the great keenness and success of insect-eating animals in their pursuit."

This conclusion does not harmonize with what appears to be the fact that only a very limited number of birds in any country, temperate or tropical, is as yet known to pursue butterflies, or that they, with the exception of the bee-eater, use these insects as a staple article of food.

Bright colors not invariably associated with a nauseous taste or odor.—While certain showy, brilliantly painted butterflies and other less conspicuously marked species are known to have a disagreeable taste or odor, there are multitudes of black or obscurely marked beetles, bugs, etc., which are still more malodorous and provided with "stink-glands." Many more detailed observations and anatomical investigations need to be made on the subject of inedible Lepidoptera. The unpalatable nymphalid butterflies (Ithomiinæ, Danainæ, Heliconinæ and Acræinæ) apparently vary in the nature and extent of the secretions. For nearly all that we know of the occurrence of repugnatorial glands in Heliconid butterflies we are indebted to Fritz Müller, who detected in Colænis, Heliconius, Eueides and Dione a pair of anal eversible glands which give out a disagreeable odor, and which appear to be the homologue of the odoriferous glands of butterflies of other groups.

[1] *Transactions Ent. Soc. London*, 1902, p. 356.

Such glands have not yet been detected in our *Anosia plexippus*. In this as in other butterflies the slightly disagreeable taste or smell is probably due to the pigment in the scales of the wings. The lepidotic acid of *Gonopteryx rhamni* is thought by Hopkins to be repellant to birds.[1]

It is well known that *Arctia virgo, Leucarctia acræa, Spilosoma virginica, Pyrrharctia isabella*, etc., secrete in eversible abdominal glands a rank, bad smelling odor which, as we have observed, is like that of laudanum. Yet these moths have no mimics, and only one of them, the Arctia, has warning colors. A few of the Syntomidæ and Zygænidæ are known to emit a disagreeable odor, as the species of Zygæna, but on tasting bits of the abdomen of a female *Ctenucha virginica* I was unable to detect any unpleasant taste; on offering one to a parrot it seized it, but let it drop and did not eat it. I do not, however, regard this experiment as a satisfactory one, as the bird may have been frightened by my attempts to hand the moth to it.

Mimicry due to convergence.—It is plainly evident that the Batesian, and more especially the Müllerian, hypotheses rests on an insecure basis and will have to be abandoned, and that the phenomena of mimicry should be attributed to convergence; certainly not primarily to the biological environment, *i.e.*, to the fancied struggle for life with insectivorous birds.

That protective mimicry is due to convergence is denied by Mr. Marshall.[2] In stating the case of *Papilio leonidas* of Mashonaland and Delagoa Bay, with its "strong and rapid flight," in contrast with the "slow sailing movements" of its southern parallel variety *brassides*, "to show off its coloration which is so characteristic of the protected Danainæ and Acræinæ," he does not attribute the difference in these two varieties to simple climatic or local causes, but to adaptation by mimicry owing to the abundance of its model *Amauris echeria*, adding: "It does not seem to me that convergence would explain the facts, for if *leonidas* is itself protected it

[1] *Phil. Trans. Roy. Soc. London*, 1895, pp. 661–682. See also Packard's *Text-book of Entomology*, p. 206.

[2] Five years' observations and experiments (1896–1901) on the bionomics of South African insects, chiefly directed to the investigation of mimicry and warning colors, by Guy A. K. Marshall. With a discussion of the results and other subjects suggested by them, by E. B. Poulton, etc., *Trans. Ent. London*, 1902, p. 507.

should exhibit throughout its range that slow flight which is the 'hall-mark' of protection, which it certainly does not in Mashonaland." We venture, however, to inquire whether climatic or local causes are not sufficient to account for the "reduction in size and number of the spots in the fore wing, and the toning down of the color from glaucous green to greenish-white, accompanied by the marked change in its mode of flight."

The changes in shape of wings and in color are probably due to the action of light and temperature, and also to the difference in amount and nature of the pigment. The cases of mimicry in butterflies of different groups, as well as in beetles, Hemiptera and other orders, seem also due to the fact that there is in day-flying insects, after all the variety of hues, a somewhat limited range of colors, and also of patterns. I am inclined to believe that these factors have so operated as to bring about the wonderful cases of convergence exemplified by the instances of Batesian and Müllerian mimicry.

In a discussion on mimicry Mr. Elwes[1] affirmed "that there was too much assumption about both the Batesian and Müllerian theories. In many supposed cases he doubted whether the so-called models were protected by taste or smell. He referred to the extraordinary superficial resemblance between two Pieridæ found in the high Andes of Bolivia and two others found at similar elevations in Ladak, Asia, and was inclined to think that similar conditions of environment produced similar effects."

Referring to Meldola's opinion that *Euplœa distanti* is the mimic of the somewhat abundant *E. breweri*, Mr. Distant[2] states that the former is found both in the Malay Peninsula, Java and Sumatra, whilst the latter is unknown to inhabit either Java or Sumatra, though plentiful in the Malay Peninsula. "Consequently in Java and Sumatra it mimics a species which does not exist nearer than in the Malay Peninsula (that is, accepting this 'mimicry hypothesis')."

Eisig has suggested, and Beddard and others have enlarged the view, that those bright colors of animals which have hitherto been regarded as of warning significance, are merely the substance or secretions which confer the unpleasant taste, and that therefore Wallace's older interpretation is unnecessary and in fact erroneous.

[1] *Trans. Ent. Soc. London.*

[2] *Annals and Mag. Nat. Hist.*, 5th ser., xi, 1883, p. 46.

We fall back on the experiments of Steinach, which demonstrate that light often acts as a direct stimulus. He glued strips of black paper to the skin of frogs which were kept in the dark; when they were exposed to the light only the uncovered parts of their skin returned to a lighter color, while the covered parts remained dark. To avoid all doubts the experiments were repeated on skin separated from the body, and photograms of letters and flowers, cut out of black paper and glued to the skin, were reproduced upon it. These experiments prove the truth of Biederman's claim that the color-cells of the frog change their shape owing to the direct action of light and temperature.[1]

The researches of Krukenberg and others show that light has a marked influence on the colors of insects; and the criticisms of Hagen, with the later researches of Hopkins, Urech, Mayer and others on pigments, all tend to show that the colors and markings of insects and other animals which by some theorists are attributed to natural selection, are really the result of the action of the primary factors of evolution, such as changes of light, heat and cold, moisture and dryness, etc., color and pattern being at the outset produced by metabolic and physiological processes.[2]

So-called warning colors in Coleoptera, etc.—Some of the so-called "warning patterns" of ground and tiger beetles, especially the former (Anthia), are claimed by Marshall and Poulton to be "very remarkable and effective." They are ornamented with large spot and stripes. When alarmed they are said to adopt a very characteristic warning attitude, and like Brachinus they eject to the distance of from four to five feet a strong acid secretion which produces a strong stinging sensation when it touches the skin of the face or back of the hands.

Here it should be observed that these spotted Carabidæ, unlike the majority of the family, are diurnal in their habits, preferring open, treeless places exposed to the direct heat and sunlight.

They are purely terrestrial in their habits, very conspicuous, and prefer an open, treeless country; they can project an acid, caustic secretion to a distance of four or five feet.

Upon looking over the beautiful plates illustrating Marshall and Poulton's interesting memoir, it strikes one that in accumulating so many examples of warning colors, they attempt to prove too much.

[1] Pflüger's *Archiv Phys.*, p. 51, 1892.

[2] See our *Text-book of Entomology*, pp. 201–210, for abstracts.

In other words, the repetition in so many insects of such different orders, often in different parts of the world, of certain colors in certain designs or patterns can scarcely be explained by attributing their appearance to the action of natural selection. Upon looking at the colored plates of Hymenoptera, Coleoptera, Hemiptera, Diptera, etc., in Marshall and Poulton's memoir, or examining similar series in a collection, where the colors are chiefly black or brown and yellow or yellow-brown, one is struck by what after all is the slight range of colors, and by the repetition of the same style of markings and of similar patterns or designs. These, being especially frequent and characteristic of day-flying, light-seeking Lepidoptera, Hymenoptera and Diptera, as well as Hemiptera, dragon flies, etc., appear to be due to the stimulus of light and shade, to high temperature, combined as a rule with moisture. These modifications and adaptations also have evidently affected multitudes of individuals in a given area; *i.e.*, all those exposed to a similar physical environment.

The claim that the markings of the Coleoptera represented on Pl. XVII, entitled "Warning patterns and mimicry of Mutillidæ in Carabidæ and Cicindelidæ, etc.," are the result of natural selection, seems rather far-fetched. The Cicindelæ in northern countries, however it may be in South Africa, are much more abundant than the species of Mutilla, and therefore less liable to be exterminated or eliminated than these rather scarce Hymenoptera; moreover, nearly all tiger beetles are day-flyers and are more or less bright colored, spotted, or adorned with metallic tints. The spotted Carabidæ are exceptional; we have spotted species in North America, and their supposed models, Mutilla, are as infrequent. We should prefer to look upon the species of Anthia figured (*A. 6-guttata* from India, *A. nimrod* and *A. omoplata* from West Africa) as simply due to convergence; the spots in the beetles and in the Mutillæ arising from the same exposure to the sun's rays in a warm country. in this case we should waive any further causal connection.

That the coloration of the Mutillæ and of the carabids cited is protective is quite evident, but we would doubt whether Müllerian mimicry is suggested or proved by the similarity of the markings of these insects. Mr. Marshall states: "The Mutillidæ of course are armed with a powerful sting, which however they are slow to use, and besides they are very hard; the red prothorax is by no means conspicuous when they are running on the ground, the abdomen being the part that catches the eye, and when hard pressed this is

elevated in the air evidently as a warning. I have noticed that it is very difficult to distinguish the pattern while the insect is running, the general impression being merely that of a black body with white spots. The same applies to the Cicindelidæ and Carabidæ, which are all fast runners and most of them very difficult to distinguish *inter se* in the field at first sight." Now we would inquire whether we need to invoke so speculative a hypothesis as the Müllerian one for these cases. Are they not almost exactly paralleled by the spots and bands of animals of numerous other orders which live exposed to the direct sunlight or to light and shade, such as the day-flying insects of different orders, spiders, the exceptionally marked rodents, myrmecophaga, chipmunk, zebra, African kudus, the tiger, leopard and other cats; in all these animals when running, leaping or flying the outlines of the body are rendered more or less indistinct by the blending of the markings. The Müllerian theory should either be extended to include all banded and spotted animals or discarded.

On Pl. XVIII, entitled "Mashonaland insects of many orders with Lycoid pattern and coloring, etc.," are sixty-two figures of as many species—"which live on flowers, are most conspicuous"—all claimed to imitate Lycus, the species of which are distasteful, and which presumably owe, according to the advocates of the Müllerian theory, their origination and preservation to this cause. All the insects on this plate have the same general yellowish-ochre hue, the end of the body or of the wings tipped or colored dark brown; a selection is made of Coleoptera of different families, of various heteropterous Hemiptera, of various Hymenoptera, such as species of Cerceris, Pompilus, and slow-flying, strong-smelling ichneumons (Bracon, etc.). How Pompilus, so amply equipped with its sting for protection against birds and lizards, should enjoy immunity from attack by its resemblance to a harmless beetle protected by its bitter flavor is not clear. The great group of Pompilidæ and allies taken the world over vastly outnumber the few scattered species of Lycus, so that in this case, as well as the carnivorous Coleoptera mentioned, to assume, as the Müllerian theory does, that such great groups, or certain of them, have come into being and maintain themselves by natural selection seems an unnecessary hypothesis. Are not the resemblances to a Lycus of the two Zygænids, which are paralleled by the American Lycomorpha, simply cases of convergence due to similar heat, dryness and other

conditions on the elevated plateau of Mashonaland? As to the supposed resemblance of the Pimplæ with dark barred wings, do they not bear quite as close a resemblance to Panorpa?

"Müllerian mimicry in South African beetles, etc.," is further illustrated by Pl. XIX, with fifty-nine excellent colored figures. The first sixteen figures represent "a powerful group of Cantharidæ and the insects convergent toward them, and having conspicuous cream, orange or red bands on a black ground." In reflecting on the causes of this similarity in coloring of Ethiopian Cantharidæ, Mylabris, etc., it occurs to one that in the humid and cool climate of the northern United States the species of Cantharis are black or gray, in the southwestern States and Territories that they become gray and spotted, in southern Europe the typical species is of a brilliant rich green, but not banded or spotted, while in Africa, with its torrid heats, these beetles though of differing genera are banded, or run into secondary forms in which the bands are broken into spots. Is there not here a direct and controlling relation to the climatic conditions, *i.e.*, heat and heat-loving habits, elevation, moisture or dryness? Whatever the style of coloration, they all secrete from the waste products of the blood a bitter vesicant pigment, by which the individuals are protected, whatever be their color, by their more than disagreeable taste and after effects.

In this plate a number of Hemiptera, yellowish or reddish banded with black, somewhat resembling the beetles, are introduced, but they are themselves distasteful and sufficiently protected unless very unlike their congeners known to be such.

The markings of beetles of various other families, Coccinellidæ, Chrysomelidæ and Cerambycidæ, some distasteful, others innocuous or neutral, are evidently the result of convergence, and the more such examples are multiplied the stronger is the case for convergence.

In the last figures (53–59) are blackish ants, with shades of reddish, *Megapetus atratus*, a hemipter, and a *Myrmecophana*? *fallax*, a cricket-like form. Now there is at first sight a general resemblance to the ants on the part of these hemipterous and orthopterous mimickers, but this is due to the loss of wings by disuse, the result of lack of exercise in flight, a cause vastly more thoroughgoing and transforming than the good or bad taste of the pigment.

Again, take the case of Belt's Nicaragua frog. All the frogs observed by Belt, with this one exception, are like those in all other

parts of the world, green or brown, imitating green or dead leaves and living among foliage, while others hide in holes and under logs. "All these come out only at night to feed, and they are all preyed upon by snakes and birds." But the single inedible species is conspicuously marked with red and blue, and it is a significant fact that it hops about in the daytime. It is apparently to this habit of living in the hot sunlight that the color markings of this frog owe their origin, driven perhaps by competition to the necessity of seeking insects in broad daylight. The sunlight and moisture of the Nicaraguan climate is perhaps with little doubt the cause of the deposition of a larger amount of pigment than in the other species; it is consequently more concentrated and acrid or nauseous, and thus repugnant to birds. We know that toads are not eaten so readily as frogs, owing to the acrid secretion from their skin. The Nicaraguan frog then, as a result of an original change in habit, became permanently diurnal, consequently the more abundant pigment, varying in thickness and density on different parts of its body, made it gayly banded and spotted, so that birds learned to avoid it. The result is that by selection, if one pleases, the species becomes established and preserved, so long as the natural conditions of existence remain unaltered. But we submit that the primary or initial causes or factors in the evolution of the so-called warning colors and taste are the result of exposure to the direct sunlight, and consequent excessive pigmentation; the food also being more abundant, as the other species are hidden away; finally we will allow that the species are preserved by what is called natural selection, though we grant this with the proviso that natural selection is powerless to act and entirely wanting and insufficient should a change of conditions, physical, climatic and biological, supervene to change the creature's habits. And so it is with the bitter-tasting butterflies and their conspicuous colors and markings; their light-loving habits and a hot, moist climate are the causes of modification—causes which cannot be overlooked or ignored.

9. Protective Mimicry not Necessarily Applicable to Snakes.

O. Boettger,[1] as the result of the examination of a collection from Brazil, finds that the prevailing colors are red, black and white or

[1] *Bericht d. Senckenberg. Naturforsch. Ges.*, 1899, pp. 75–88. Also *Journ. Roy. Micr. Soc.*, 1900, p. 311.

yellow, arranged in certain definite patterns. Of eight species of Elaps and the same number of species of harmless snakes, the latter "mimic" the Elaps.

But in India where three poisonous genera are mimicked by three harmless genera, the poisonous, however, prey on the mimics; they are not protected except from birds.

10. Müllerian Mimicry not applicable in certain cases even in Butterflies.

Mr. G. F. Matthews, visiting the Solomon Islands, writes: "A very interesting case of mimicry occurred here. A dark brown Euplœa with broad white outer margins, and *Danais insolata* with markings almost identical, were fairly plentiful; but, to add to the confusion of things, a Hypolimnas, which on the wing might have been mistaken for either, was flying with them. Which mimicked which it was difficult to say, or the reason of the mimicry, as all three genera are avoided by birds both in the larva and perfect stages. The theories of Müller and of Bates have been strongly maintained by ultra-Darwinians; but there is on the part of some who have seen how seldom birds seem to care to chase butterflies of any kind a feeling that the theories in question have but a limited basis of fact."

Sir George F. Hampson discusses in *Nature* what he aptly calls "museum mimicry." "It was," he says, "recently stated by Colonel Swinhoe that Danaid butterflies are mimicked, as a means of protection, by three genera of the Chalcosia group of moths." But it appears that the latter secrete strong acrid juices, as does the whole family to which they belong, while they are so distasteful that hardly any other animals will touch them; their habits too are very different from those of butterflies, and no one, he says, who knows them could possibly believe in protective mimicry between the two groups.

11. Indifference Shown to Butterflies by Birds.

It appears to be the case in Europe that birds actually reject or at least are indifferent to butterflies, and this seems to be the case in the United States and Canada, judging from the facts now known, and my own slight observations. Birds will as if in play dart after butterflies, as they will after a flying leaf, but will not devour them, while they will catch and eat moths.

Thus Irmscher[1] states than on setting free a large number of common Noctuids (species of Agrotis and Leucania) most of them were eaten by the redstart resting near by. But it was remarkable that of the numerous *Vanessa io* which he set free, not a single one was caught by the redstarts.

Dr. A. Seitz[2] records having seen Pieris make a rush after the feathers of birds and bits of paper which had fluttered down in the air. He saw a young wagtail pursue a *Colias hyale;* it rushed after the butterfly, which fell to the ground, but the bird then flew at least four or five times over the prostrate butterfly without taking any further notice of it whatever. From this observation he infers that the insectivorous birds in Europe are indifferent to or disdain butterflies, and he goes on to theoretically prove that butterflies are not molested by birds. Undoubtedly the irregular wavering flight of butterflies enables them to escape the occasional onset of birds. Thus Seitz states from his observations that the kind of flight of Lepidoptera has a good deal to do with the matter. The males of several species of moths (*e.g., Gastropacha quercus*) whose flight is irregular, restless and fluttering, are not followed by birds, which will devour the females whose flight is more steady.

12. Sokolowsky's Views on the Origin of the Markings of Mammals and the Formation of Spots from Longitudinal Stripes.

In his interesting paper Sokolowsky[3] has been the first to thoroughly discuss the markings of mammals. He contends that the most primitive style of markings are longitudinal stripes developed in small ground mammals, and caused by the long, slender shadows of the fern vegetations of the ground-zone of the primitive forests. In the larger animals of the bush-zone there appeared a change of markings, due to the play of light and shadow in the plants of this zone. Such are Centetes, Geomys, Tamias or the chipmunk. In *Cœlogenys paca* the five rows of round white spots on each side are due to the breaking up of the originally five stripes into spots. The greater variety of plants in the bush-zone formed a chaos of contrasting light and shade, so that the markings of these or similar mammals

[1] *Illust. Zeit. Ent. Neudamm.*, V, p. 75, März, 1900.

[2] Spengel's *Zool. Jahrbücher*, iii.

[3] Über die Beziehungen zwischen Lebensweise und Zeichnung bei Säugetieren Zürich, 1895.

became adapted to it. "Nature," he says, "has settled this question with masterly skill. She dissolved the longitudinal stripes into spotted markings by interrupting the separate longitudinal lines. . . . . The advantage of this kind of marking is this, that the whole impression of the animal's form is broken up by the many interruptions of the ground coloring by means of the spots, and therefore the particular animal is lost to sight in the confusion of light and shade in the forest."

This process of development of spots is especially seen in the Carnivora and more particularly in the Viverridæ, which date back to the Miocene Tertiary. These forms still possess the traces of the more primitive longitudinal striping, as seen in *Viverra schlegeli*, in which there are plain longitudinal dorsal stripes. In *Viverra indica* the spots are arranged in longitudinal rows, which are still partly connected on the back, and form short longitudinal lines. In *V. genetta* are traces of the primitive longitudinal lines. All these animals prefer bushy regions. The larger Carnivora, *i.e.*, the Felidæ, inhabit not the deep, dark forest, but the edge of the woods near the banks of the rivers, where they have become adapted in coloration to the "luxuriant chaos" of lights and shadows. "As eye-witnesses report, the form of the leopard, for example, is so dissolved by means of the variegated parti-colored ring-like markings that it becomes difficult even for the accustomed eye of a native of these regions to perceive the animal in the leafy confusion." The evolution of the ringed marking has perhaps originated from both forms of marking, the longitudinal stripes and the spots, and is discussed at some length by the author. He supposes that the rings are caused by a subdivision of the single spots. Thus in the ocelot the longitudinal stripes may have split lengthwise and formed rings by their falling apart into sections which again divide into dots. Whether the markings of the tiger arose from the dissolving of the horizontal cross partitions (seen in *F. nebulosa*) or were formed by the blending of spots lying on top of each other is, he thinks, an open question, yet it is a fact that the markings of the tiger show rings which are arranged both vertically and lengthwise. Eimer regards the transverse stripes as due to a blending of the spots in a vertical direction. The origin of transverse series of spots from longitudinal stripes is clearly seen in the ontogeny of *Datana major*. (See my monograph of bombycine moths, Pt. I, Pl. XII, and Pt. II, p. 8, 1905.)

On the other hand arboreal mammals, as the squirrels, tree monkeys, etc., have lost their primitive markings, so that we have in them an entire group of unmarked species, or what markings are left are confined to a ring on the tail, and to shorter or longer stripes on the forehead and back; such are Nasua, Procyon, Ailurus, Bassaris, *Lemur calla*, several species of Hapale, as also *Cebus leucogenys*.

Leaving the tropical forests, Sokolowsky then considers the style of marking of those mammals inhabiting steppes, prairies surrounding the edge of woods, savannas, pampas, and finally deserts. He confines himself to the steppes of middle and southern Africa, with their often rich vegetation and great seasonal changes, so that the mammalian life has become adapted to the most varying and strict privations and necessities.

In the mammals of the grassy steppes or plains, while originally migrating from forest and bush regions, the markings have undergone a process of reduction, and there are two styles of markings, *i.e.*, the dots and the diagonal stripes. Martin alleges that the form of leopard frequenting the extensive grassy plains of the flat Nile lands has a dotted coat suggestive of the markings of the geparde. The sleek spotted mammals of the steppes also show similar modifications in markings. *Felis serval*, although it conforms most closely to the forest forms, still shows even on the back of the head and on the shoulders four longitudinal black stripes which are certainly mingled with spots, whereas on the cheeks occur small spots recalling the dots of the geparde, those on the side of the body being larger. The spotted hyena (*Hyæna acuta*) lurks on the edges of the deserts, and it presents many climatic variations differing in color and markings, while the sojourn in the steppes has produced an irregular arrangement of spots. The uniformly dusky-toned ground-color of its coat so blends at nightfall with the irregularly placed spots that it may be justly regarded as a twilight clothing.

Sokolowsky here refers to the fact that each style of marking, however varied in color in the daytime, yet at the appearance of darkness is so combined with the ground-tone of the coat and with the surroundings that a protective clothing is provided at night also.

Mammals which are notoriously nocturnal in their habits are generally destitute of markings, as are the burrowing mice and rats which live on the ground in Northern Africa.

The giraffe has a special kind of spotted marking. The large

irregularly situated spots lie so close together that the ground-tone of the coat looks like network. Stanley discovered in Central Africa a variety with large round black spots. The giraffe has been observed to strikingly resemble the dead lichen-covered trunks of last year's mimosa trees, so as to be mistaken for them. (Also see Wallace's *Darwinism*, p. 212.) This spotted style of marking merely results, adds Sokolowsky, from a splitting of the original longitudinal stripes due to the great size of the animal. The variety with dark markings is indisputably nearer to the earlier forest form than to the lighter colored form.

He considers that the lion has descended from ancestors with a ringed kind of marking, as in quite young stuffed examples there are ring-like spots on the body. Here we might add that we have observed in the young panther (*F. concolor*) when three months old that the coat is distinctly spotted, showing that it originally was a forest cat, becoming afterward adapted to a life on treeless plains.

The markings of the zebras, asses and wild horses, as well as antelopes, are discussed at length, the effacement of the primitive stripes being attributed to a life on grassy plains. The Canidæ are supposed by our author to have originally been more or less transversely striped, cases of partial dorsal striping in *Canis mesomelas*, *C. azaræ*, *C. lupus*, and others being attributed to reversion.

In foxes this is seen, especially the cross fox, which bears a dark dorsal stripe with darker transverse bands on the shoulders.

13. Pœcilogeny in Zebras and African Antelopes due to the Action of Light and Shade.

As has been observed by several hunters and naturalists, the zebra is rendered nearly indistinguishable, when swiftly running, by the blending of the bars and stripes. Prof. Ewart states that the lion is the most inveterate enemy of the zebra, which is protected by its style of coloration as well as the rapidity of its movements. There is no animal, he says, which could turn about and break into a trot so quickly as the zebra. He points out that the stripes of the zebra are undoubtedly protective, causing the animal to become indistinguishable at a comparatively short distance. This he has experimentally proved by tying ribbons upon a dun-colored pony so as to break up the uniform coloration, the result being that the pony thus rendered zebra-like in its stripes was similarly indistinguishable.

Mr. Pocock has clearly shown that the stripes and bars of zebras and antelopes are in close relation to the environment of these animals, and that the stripes and spots are the result of light and shade. In *Nature* for August 13, 1903, p. 356, he states that Grant's quagga, which inhabits northeastern Africa, is one of the most completely striped of existing horses. It is, he says, a mass of stripes from head to tail, from hoof to spine. Intermediate forms connect it with Gray's quagga of Cape Colony, which has pale stripeless limbs, under sides and hind quarters. Now a series of three local races lead from Grant's to Gray's quagga. The tendency of these modifications is to convert a striped and conspicuously parti-colored animal into one which, even at a short distance, must have appeared to be an almost uniform brown, paling into cream on the under side, limbs and back of the haunches.

A zebra, he says, has such a coloration as to render it invisible under three conditions, *i.e.*, at a distance in the open plain in midday, at close quarters in the dusk and on moonlit nights, and in the cover afforded by thickets. The white stripes blend with the shafts of light sifted through the foliage and branches and reflected by the leaves of the trees, and in an uncertain light or at long range they mutually counteract each other and fuse to a uniform gray. Also the alternate arrangement of the black and white bars contributes something to the effect produced, by imparting a blurred appearance to the body.

The asses of northeastern Africa are perfectly adapted to their surroundings in color, and so with the kiang and with Prjevalsky's horse of Central Asia. Their coloration and the resulting protection is explained by Thayer's theory or law of the counteraction of light and shade. Pocock gives a good example. When the Asiatic kiang or the quagga of Cape Colony lies on the ground in the attitude characteristic of ungulates, the white on the back of the thighs is brought into line with that of the belly, and a continuous expanse of white, obliterating the shadow, extends all along the under side from the knee to the root of the tail. "In correlation with the adoption of a life in the open, a new method of concealment by means of shadow counteraction was required, and was gradually perfected by the toning down of the stripes on the upper side and the suppression of those on the hind quarters, belly and legs." The same style of markings occurs in many antelopes, gazelles and in the bonte-bok. They need to be thus concealed when lying

down and chewing the cud. When they are in motion the white rump may act as "follow-the-leader" or as danger signals, and Pocock thinks they are not necessarily recognition marks.

In his interesting article entitled "Antelopes and their recognition marks,"[1] Mr. Pocock regards the face and foot markings as, like the stripes, "representing spots or streaks of sunlight passing through foliage or reflected from leaves." Accepting Thayer's hypothesis of concealment by the counteraction of light and shade and applying it to the lesser kudu, "it will be seen," he says, "that the white is laid on where shadows are thrown; that the white rim on the upper lip and the white chin must counteract the shadows caused by the fold of the mouth and by the muzzle; the two white blotches on the neck must counteract the shadows thrown by the head and by the curvature of the throat, and the shadows cast by the breast and groin must be similarly obliterated by the white patches on the inner side of the base of the limbs."

That the markings or their absence are the result of adaptation to the environment is clearly established by the examples given by Pocock. The markings of the African elands are correlated with their habits, there being "a complete gradation from the strongly marked forest species through the weakly marked species frequenting the open bush to the unmarked desert species." The kudus illustrate the same principle. "Both the species of kudu are well marked with white stripes on body and head, but the smaller (*S. imberbis*) is much more strikingly marked than the larger (*S. strepsiceros*), having more stripes on the body and two patches on the throat. In Somaliland, where both species occur, the larger lives, according to Swayne, in the mountains, on very broken ground where there is plenty of bush; and sometimes indeed ventures into the open plain (Inverarity). The lesser kudu, on the contrary, is 'found in thick jungles . . . . especially where there is an undergrowth of the slender pointed aloe which grows from four to six feet high' (Swayne). Evidence of a like kind is furnished by other species of Tragelaphines. . . . . The beautifully marked nyala (*T. angasi*) and bongo (*T. euryceros*) live in dense thickets; and the lovely little bush-bucks (*T. sylvatica, scriptus*, etc.) seldom venture out of cover except at night time to feed. On the other hand the nylghaie, an aberrant member of the same tribe, is without body-stripes, and lives for the most part in more or

[1] *Nature*, Oct. 11, 1900, p. 584.

less open country in India, and is not a typical denizen of the jungle at all."

Pocock supplies another set of facts, showing the coexistence of white marks with long ears of zebras and antelopes and a bush life, bearing out the supposition that the marks, like the ears, are primarily for protection.

"The markings take the form of strongly contrasted bands of white and black or brown. Objects banded in this way are as a rule more, and not less, difficult to see in their natural surroundings than those that are uniformly colored. There is little of the gloss on the coat of a gray or white horse that is seen on a bay or black, because white hair reflects the light less vividly than dark. Hence alternating bands of these hues impart a blurred irregular aspect to a body, destroy the apparent evenness of its surface and break up the continuity of its outline. In an uncertain light a zebra's stripes merge 'into a gray tint,' and naturally counteract each other, so that the animal is nearly invisible"

Pocock also, as Thayer, insists that for concealment perfect stillness is of all things most important. "Movement means detection, and detection may mean death." Hence protective markings on the face are important, and he presumes that the pair of sunlight patches on the tiger's face increases its chances of concealment when watching for prey or creeping toward it.

This is confirmed by hunters. Mr. M. E. Robertson, of Chocorua, N. H., in shooting a deer on the edge of Chocorua Lake, entirely overlooked another one still nearer, within fifteen feet of the road, which stood perfectly still, being only partly concealed among the trees and bushes until it moved and was seen. The white markings on the face, around the eyes and on throat, as also on the inside of the large ears of our deer, serve, as in the cases of the deer and antelopes of other continents, to make the head blend with the lights and shades of the foliage in which it stands.

14. Blending of the Stripes of the Chipmunk.

In this conspicuously striped squirrel there appears to be a blending of the stripes when the animal is swiftly running. Although I have frequently seen this species running, I confess I have not clearly seen a partial obliteration or blending of the stripes; in the most favorable instance the animal ran from me so swiftly that it was not possible to tell whether or not the stripes blended.

Several of my students whom I asked about the matter, after showing them a stuffed specimen and explaining the theory of blending, have related their experience. Mr. C. A. Weeks tells me that he noticed a blending of the stripes while seeing a chipmunk running. Mr. T. McA. Webb reported that the chipmunk when running "appears all one color." Mr. J. H. Breslin writes, "I have often gone shooting for chipmunks, and found it very difficult to shoot one because it is so difficult to see it. I have often seen them on the rails of fences, and when you look right down upon one, it looks like part of the rail."

Mr. T. E. B. Pope tells me that "when the chipmunk runs slowly the black stripes are very distinct, but when running rapidly the dark stripes along the back appear to blend, so that the back appears dark as compared with the reddish or chestnut color of the under side; there is a black mass above and a chestnut mass beneath."

Mr. Glover M. Allen writes: "I have never looked particularly for the blending of stripes in the chipmunk as it runs, but my recollection would be that the stripes are not distinctly seen in rapid movement, and the general effect is of a brownish animal." He tells me that he has since observed that when it runs slowly the white stripes are distinct, but the dark ones less so.

Mr. W. J. Long writes me: The effect of the stripes is when it is running to make a *blur* of the animal, making it a difficult object for hawk or owl to hit. I used to try sighting a gun or rifle at chipmunks (not to shoot, for I am especially fond of the little creatures) and was surprised to find how hard it was to catch him with the head, much harder than a running red squirrel for instance. The stripes also help it when it is sitting still, for it gives at times the curious effect of sunlight streaming down between the leaves or twigs making bars of light and shade. The same results of the stripes may be noticed in young woodcock, as mentioned, but not carried out, in my "Little Brother to the Bear."

I also inquired of Mr. Abbott H. Thayer whether he had observed the blending of the stripes, and he kindly wrote me as follows:

"Chipmunks, like the vast majority of mammals and the whole animal kingdom, with exceptions almost wholly confined to male birds, are graded from dark above to white beneath in exactly the degree to efface their appearance of normal rotundity, and hence

like all objects so graded inevitably lack appearance of solidity, so that their resultant color passes for a part of their background. Stripes, dots, and all other patterns which are found participating in this graduation in most animals that live where their background is diversified with corresponding *degrees* of pattern (as it is in the forest by twigs, dead leaves and little dark holes and the shadows along the under side of light colored twigs) are simply a sort of resultant picture of the average background, just as high-swimming fishes like herring, pompano, bluefish, etc., having no patterns in their background have none on their coats. Chipmunk's stripes are very good rendering of horizontal twigs lighted from above and seen against a more distinct ground." (Also see p. 445).

15. Protective Coloration and Blending of the Markings in the Sandpeep.

After writing this paper I had the opportunity of observing on the Maine coast, September 3, a flock of sandpeeps which were very tame and allowed me to approach in my skiff within a few feet of them. At the distance of from about seventy-five to one hundred feet I could scarcely detect them as they were slowly walking over a little beach of coarse dark gneiss pebbles, the upper part of the oval body being of the same hue as the pebbles; it was only when within from forty to thirty feet that they could be clearly distinguished; it was a clear case of obliteration. On the other hand when standing at the level of my eyes on a dyke of feldspar, their whitish under side blended with the rock when resting, but on the dark gneiss rock enclosing the dike they stood out distinctly.

The flock was made up of old birds and young ones, the latter so tame that I could approach them in my skiff within about four feet.

When flying away they reminded me of the hawk-moth, *Deilephila lineata*, the bars on the wings and neck blending in the same manner, yet the dark and white bands on the body of the young birds remained distinct in slow flight.

The stripes and bars of no value as recognition marks.—Without entering at length into a discussion of Wallace's theory of recognition marks, which it seems to me has been effectually disposed of by Pocock, it at once struck me in watching these birds on the wing that the light and dark bars and rings so far from being distinct, and thus serving as recognition marks, actually so blended as to make the bird's shape less distinct, and thus the markings were

of no avail, producing the contrary effect of rendering these birds unrecognizable by their own species. And this it is obvious will apply to any birds and beasts similarly marked. Yet it may be that the white rump of deer, etc., may when the creatures are walking or slowly running serve as a guide to those following, as allowed by Pocock.

16. Blending of Black and White Bars in Moths, Butterflies, etc.

Blending of the bars in moths.—The flight of certain species of geometrid and pyralid moths, which are black marked with broad white bands, many years ago attracted my attention. When any of these smaller moths, such as the geometrids mentioned below and *Desmia funeralis* and other black and white Pyralids, are rather rapidly flying away from one the singular effect is that of whirling incomplete black and white broken circles, making the outlines of the body and wings confused, which, added to their irregular flight, renders them difficult to catch.

I well remember when on the Labrador coast in 1864, where the geometrid moth, *Rheumaptera hastata*, was abundant, flying in considerable numbers, the peculiar effect on my mind of its flight. This moth has broad black wings, marked with conspicuous white bands or bars. It ranges from the Arctic regions to Maine. In its uncertain devious flight the effect of the moth in its not particularly rapid flight was that of black and white incomplete and confused rings circling through the air. This partial blending of the white and black bands, added to the zigzag, uncertain flight, would make it very difficult for a bird to follow and seize such insects, which when disturbed fly by day and are thus protected. There are several other boreal or Arctic geometrids similarly marked, and also the species of Heliommata and Euchœca (Baptria).

Blending of the black and yellow stripes of Papilio turnus.—On June 22, 1902, at Brunswick, Me., I for some time watched this butterfly leisurely flying from flower to flower. It seemed to me that during its flight there was a slight blending of the pale yellow orange of the wings with the black ground color, so that the general effect was that of pale yellow. A member of my family independently noticed the same blending and corroborated my own observations. She noticed that the black borders of the wings were rendered less distinct by the blending of the series of round yellowish

spots. The above was written out at the time, but my later experiment with the rotating wheel (p. 445) quite satisfactorily corroborates my observations.

Blending of the bars and lines in Deilephila lineata —Early in September I observed at Sugar Hill, N. H., one of these hawk moths flying over and probing the flowers of the sweet william, of which it seemed especially fond, and paying little attention to the candytufts, petunias and marigolds in flower in the same beds.

During its rapid flight the bars or stripes and lines on its wings certainly blended, rendering the outlines and markings of the wings in their swift motion blurred and very indistinct, with no definite outline. The bars on the outstretched wings are parallel with the transverse bars or rings on the abdomen, the latter being more distinct, as also the longitudinal ones on the back of the thorax. The circumstances then reminded me of the statements regarding the blending of the stripes of the zebra, and the effect was such as to plainly make the moth invisible, or at least much less easily seen and caught by birds.

I also on the same day observed another of the same species on the other side of the road visiting red clover, etc., and my observations (written as here the same day) were corroborated by a member of my family.

Blending of the bars in a dragon fly.—On June 27th of the present year I watched a *Libellula trimaculata* flying in my yard. The wings are whitish, with a broad dark brown middle patch, the abdomen being a hoary whitish gray, and very conspicuous.

During its flight it seemed to me that the colors blended so as to make it more indistinct when more swiftly flying. The observation needs however to be completed, yet this dragon fly is a capital case for further examination.

17. Abundance of Markings in the Life of Coral Reefs.

In a lecture delivered at the London Institute on the animal life on a coral reef, Dr. S. J. Hickson said that the richest fauna in the tropics is the region which extends from the growing edge of the reef to a depth of some ten or fifteen fathoms beyond it. And here it is that the struggle for existence is most severe, where the animals are protected and concealed by the most pronounced marks and colors, and provided with stings and spines to defend them in the battles with their enemies. The crowded life appears to be

primarily due to the *abundance of light and heat*, there being no great or sudden changes of temperature or of the chemical composition of the water; while there is an abundant food supply brought by the tidal currents from the surface of the ocean. Prof. Hickson thinks that the brilliant tints, spots and stripes seen on polyps, prawns, octopods and fishes are due to the fact that they live among the brilliant surroundings of the coral reef: "or, to put it in another way, animals similarly organized and of similar habits would be at a disadvantage on the coral reefs if they were not so marked and colored." The other fishes of the tropics, he observes, do not possess these curious and beautiful characters; the sharks, bonitos, flying fishes, herrings and others that do not live habitually on the coral reefs are not unlike in general color and ornamentation the fish of temperate seas. Hence, these characters of coral-reef animals are *not directly due to the high temperature and bright light of the tropics, but are due to the character of the surroundings*. He adds that most of the tints are concealment colors. The only example of what appears to be a warning color that he noticed occurs in connection with the spines on the tails of certain surgeons and trigger fish. *Acanthurus achilles*, for example, has a uniform purple color, but there is a bright red patch surrounding the formidable tail spines that give these fish the name of surgeons. Similar warning colors are very pronounced also in *Naseus unicornis* and *N. lituratus*, and in some of the Balistidæ.

18. The Lack of Color-Patterns in Deep-Sea Fishes and Crustacea as contrasted with those of Shoal Sunlit Waters.

Alcock, in his *Naturalist in Indian Seas*, states that the majority of deep-sea fishes are of uniform usually sombre color, only a minority in that ocean being banded, striped, or otherwise marked in definite patterns. To enter into details: of 168 species dredged below the 100-fathom line, fifty-two were black or some shade of blue or purple-black; fifty-six were dull brown; ten were silvered over a blackish or brownish ground color; ten were bright silver; four gray—thus 78 per cent. were simply-colored species. Fourteen species living between 100 and 250 fathoms were nearly uniform red or of a rosy hue. Only eighteen species, and those dredged near the 100-fathom line, were striped or marked with patterns, and only four were brilliantly variegated with many colors.

Colors of Deep-Sea Crustacea.—Alcock also remarks that while in the decapods dredged in abyssal waters the colors were red, pink, orange, yellow, a few brown, purple and white, none were spotted, striped or with variegated patterns. Thus they entirely differ from shallow-water forms with their freaks of color or labyrinthine mottlings and dapplings.

19. Thayer's Law and His Experimental Proof.

In a suggestive article on protective coloration Mr. Abbott H. Thayer[1] considers the subject from an artist's point of view. "Animals," he says, "are painted by Nature darkest on those parts which tend to be most lighted by the sky's light, and *vice versa*." The prevalent idea of protective mimicry, he says, makes an animal appear to be some other thing, whereas it makes it cease to appear to exist at all.

The colors of the ruffed grouse are a complete gradation from brown above to silvery-white beneath. It grows light under the shelving eyebrows and darker again on the projecting cheek. When it stands alive on the ground its obliteration by the effect of the top light is obvious. By extending its protective color all over it, treating the under side with brown to match its back, the bird was made distinctly visible.

Thayer proved this by the following experiment. He had about a dozen egg-shaped pieces of wood made of the size of a woodcock's body. They were mounted on wire legs to poise six inches above the ground. Most of them he painted in imitation of the color gradation of a grouse or hare—earth color above to pure white beneath—while to two others he gave a coat of earth color above and below. He then set the whole lot like a flock of shore birds on the bare ground in a city lot, and invited a well-known ornithologist to look for them at a distance of from forty to fifty yards, who at once saw the two monochrome ones, but, although told exactly where to look, he failed to detect any of the others until within six or seven yards of them, and then only by knowing exactly where to look. He also painted bright blue and red spots on the brown back of one of them, which spots only passed for details of the ground beyond the egg.

[1] "The law which underlies protective coloration," *The Auk*, xiii, April and Oct., 1896. Also *Smithsonian Report* for 1897, p. 477.

In his second paper[1] Mr. Thayer points out that the coloration of every individual of the "mimicking groups" of butterflies seems to be the best conceivable for effacing the aspect of its wearer. "Most animals," he well says, "wear on their coats pictures of their habitat." "As I before pointed out, even the under side of the wings and tails of hawks bear the general twig patterns so common on forest birds, as if Nature found it worth while to efface the white silhouette their wings' under sides would make when they extended them while perching. We see how completely such patterns (when couched, of course, as they always are, in the effacive gradation) *do* help to obliterate a partridge, grouse, woodcock, hare, or any other of almost all the species in every order; since they prove to be actual *animated pictures* of their environment. As I said before, in my paper on so-called 'Banner-marks,'[2] these forest-like patterns are found on forest creatures, and not on desert creatures or ocean creatures. Sand birds are usually marked in longitudinal, delicate patterns, very like those the sand assumes when seen at the same angle at which one observes the birds themselves. Tigers and zebras are resolved into pictures of tall, strong flags, grasses and bamboos, while the lion is a picture of the desert. (It will some day be plainly understood that the effacive gradation is the essence of the success of these patterns. Were they not arranged to compose one perfect counter gradation, from top-dark to under-white, they would appear merely as what artists call 'lines of quantity,' like the hoops of a barrel, *emphasizing* the rotundity, not effacing it.)"

Butterflies, he claims, are "mainly either flying pictures of various combinations of flowers and their backgrounds, pictures of the *shadow under foliage*, with delicate patterns of vegetation or flowers drawn across it, as, for instance, in the North American *Papilio polydamas* and the dark Satyrinæ, or that they are wonderful representations of flowers themselves, as in the Pierinæ." He also claims that "*any* pattern is less conspicuous than bright, unshiny monochrome."

He likewise briefly recognizes the effect of rapid movement in

[1] "Protective coloration in its relation to mimicry, common warning colors and sexual selection," *Trans. Ent. Soc.*, London, Dec., 1903, pp. 553–569. The copy kindly sent me by Mr. Thayer has some valuable emendations and additions.

[2] *The Auk*, xvii, 1900, p. 108.

obliterating patterns. "The act of flight tends to obliterate patterns, by the too quick substitution of one color for another before the eye. A black and white butterfly, therefore, tends to look simply *gray* in swift flight."

20. Experiments on the Obliteration of Bars and Spots with Bradley's Color Wheel.

The following experiments on the artificial blending and obliteration of stripes and spots, by means of a revolving disk covered with parti-colored stripes or spots, throw, it seems to me, much light on this subject and satisfactorily proves that the stripes, bars and spots, contrasting with the ground colors of moths, butterflies, fishes, reptiles, birds and mammals thus marked, must necessarily blend so as to render the outline of the animal indistinct when it is in rapid motion.

I covered a six-inch black disk with squares of white paper about a quarter of an inch wide, in imitation of the squarish white spots on a loon's back. Moving the disk slowly there resulted three quite distinct black rings about a quarter of an inch wide, separated by white rings. When the wheel was revolved at full speed the black ground color and white spots all blended into whitish pearl-gray, of the general color of the under side of the loon's body. The white spots certainly all produced a decidedly blurred, indistinct whitish pearl-gray tone. It is thus probable that the loon's back during rapid flight harmonizes with the neutral gray of the sky, especially in cloudy weather, and tends to either obscure it or render it more or less invisible.

On a white disk was then pasted a series of wide dark brown stripes, in imitation of the stripes on a zebra. On rapidly revolving the wheel the stripes and ground color blended into a grayish-white or neutral tint. On a six-inch black disk were pasted three sinuous white bands from a quarter to half an inch in width, one white band on one side one inch long and that on the opposite side five inches long. When the disk was slowly revolved the black and white stripes blended, but there were visible two darker rings; but when the wheel was revolved more rapidly all perfectly blended into a whitish-gray hue like the color of the sky. This shows that the stripes of a zebra when in rapid motion would be blended, and its outlines rendered more or less indistinct, in accordance with the statements of different hunters and naturalists.

It will be remembered that on the outer margin of the wings of *Papilio asterias* there is a row of rather large round yellow spots on a black-brown ground. I pasted near the edge of a six-inch black disk several roundish dark buff spots nearly an inch in diameter. On revolving the disk, the spots formed a wide dark yellowish-gray band. The result was that the edge of the disk was made indistinct; the same effect is apparently produced by the yellowish spots on the butterfly's wing. A member of my family noticed that in a Papilio thus ornamented the outline of the wings was during flight blurred and made indistinct. Also the ground beetles Anthia and others, the Cicindelidæ and Mutillidæ are ornamented with large conspicuous yellow dots or spots which probably more or less blend.

I stuck on the same black disk five one-half-inch buff bands. On slowly turning the wheel two black rings were formed, the ground color of the disk being dark buff; on more rapidly turning the wheel a general dusky buff hue pervaded the disk.

In revolving a half or a three-quarters black disk over a white one the colors blended into gray. A disk half green and half black formed a darker green, and a disk three-quarters green and one-quarter black blended into a slightly darker green. A disk one-half or two-thirds yellow, the rest Venetian red, upon revolving produced a deep orange hue. A disk three-quarters yellow and one-quarter Venetian red produced an ochre-yellow, less deep than the orange effect. On revolving a disk one-half blue and one-half yellow a royal purple hue resulted.

From these experiments it appears to result that in any striped or spotted animal, when rapidly running or flying, the stripes or spots must inevitably tend to be confused or blended; and when the ground color and stripes or spots are of opposite hues, as black and white, the result will be a pearl-gray or cloud-like neutral tint, thus obliterating or at least obscuring the outlines of the body. Thus birds like the loon, pigeons with their barred wings, moths and butterflies with striking bands of very different hues, the tiger or zebra with its stripes, and the ocelot with its spots, tend when rapidly moving to become obscured to the vision, and to harmonize with the earth or sky.

The following experiment was less satisfactory than the foregoing. I fastened a stuffed chipmunk with its back upward on the outer edge of a large disk of white pasteboard. On revolving it slowly on

a color wheel the stripes remained distinct, not blending. When the speed was increased to a degree evidently exceeding that of the animal in its swiftest movements, it formed a dark grayish-brown, almost black ring, and the stripes were nearly if not wholly blended, certainly enough so to render the animal inconspicuous. One would expect that as the ground color of the chipmunk is a russet or reddish-brown the ring would be russet or reddish-brown, but this was not the case.

The animal was then placed on its side and so attached to the white disk that the subdorsal whitish stripe was visible, and also the upper portion of the light under side of the body. On rapidly revolving the disk the lighter and darker portions of the chipmunk still remained somewhat distinct, not perfectly blending. The result was a blurred, confused mass lighter on the under side and darker along the back.

The experiment was not so satisfactory as those with the zebra markings, and it is hoped that some one will make further experiments. The direction of rotation was parallel with that of the striped body of the chipmunk. There are in this animal no transverse bars, hence the stripes do not so readily blend. Moreover the body of the animal in running is more or less unsteady, undulating or arched. Until further observations are made we would provisionally conclude that the stripes of the chipmunk remain distinct when the animal is slowly running, but that they become blurred or confused when the creature is darting off at its greatest speed.

21. Pœcilogeny in Paleozoic Times.

In claiming that all Müllerian mimicry is due to the attacks of birds, one would do well to bear in mind that a number of paleozoic net-veined insects had wings which were banded or spotted, and that these insects lived at a period when modern lizards, much less birds, did not exist. It may therefore be inferred that these markings originated from the simple action of physical and physiological causes, irrespective of the biological environment, such as the attacks of insectivorous animals, unless they suffered from the desultory warfare waged by the small active terrestrial labyrinthodents, such as the Hyalonema, etc., of the Upper Carboniferous period of Nova Scotia.

If we examine the works of Brongniart and of Scudder on fossil insects it becomes apparent that pœcilogeny was an active process as

early as the Carboniferous period. The wings of many net-veined insects were then not only barred but spotted and ocellated as completely and beautifully as those of insects at the present time.

Wings banded.—Among those with banded wings were *Protophasma dumasi*, whose wings of both pairs were marked with six large parallel dusky bands. The wings of *Brodia priscocincta* were ornamented with three broad transverse bands or series of spots of a dull umber brown color. On the wings of *Lithomantis goldenbergi* were broad shades, the outer half of the wings being shaded.

Wings with solid spots.—Of the known species the great number of those ornamented at all already had the wings well spotted, showing that the process of specialization or division of stripes into spots had already been active, perhaps during the Devonian period.

On the wings of *Becquerelia superba* and of other species there are traces of at least seven rows of large spots. The wings of *Spilaptera packardii* were much spotted, the spots being large and oval, situated in the cells, with ten costal spots on the inner half of the wing; all the spots being arranged in about twenty-two series very oblique and parallel with the veins.

Nearly all the Carboniferous primitive Ephemeridæ had wings as well spotted as those now existing. In some kinds the wings were actually more numerously banded and beautifully spotted than any now existing. In *Sphecoptera gracilis* the wing is crossed by nine rows of large spots. In *Fouquea lacroixi* there are eight sets of large pale blotches, two or three in a row. *Palæoptilus brullei* has wings crossed by six rows of very large blotches, two in a row.

Ocellated wings.—In *Lamproptilia grand'euryi* the wings bear large somewhat eyed spots irregularly arranged. *Psilothorax longicauda*, an Ephemerid, is ornamented on the fore wings with at least twelve rows of ocellated spots.

In insects of the Oligocene tertiary age the wings were banded much as in existing insects. Thus in *Phryganea antiqua* the fore wings were crossed with eleven broad parallel bars; and *P. fossilis* had nine bars.

22. Keeble and Gamble's Studies on the Origin of Markings of the Shrimp.

That stripes and bars are due to the lights and shadows of a forest or grass land is the opinion of the authors we have quoted in these pages.

Much light, it seems to us, has been thrown on the actual mode of origin of stripes and bars in general by Keeble and Gamble[1] in their valuable essay on the color physiology of the higher Crustacea. They hold that the adult color pattern of *Hippolyte varians* "is determined by the environment and not inheritance." "The adult pattern arises in spite of difficulties which are thrown in its way. Gaps are bridged over, stripes are evolved, stripes are made to bars, and bars blend to a monochrome." How a bar is formed by a bar of shadow is thus stated :

"We know (see Section IX) that the pigments of the chromatophores expand into the branches under certain conditions of illumination (*e g.*, on dark background) and contract into the centres in diffuse light. Imagine a practically transparent Hippolyte (such, for example, as the earliest adolescent faint brown-lined forms) resting persistently, as it does rest, in such a situation that a bar of shadow falls across it, whilst over all the rest of its body light falls. In the region of the bar of shadow the chromatophores will expand. In the rest of the body they will be contracted to mere dots. Grant that where the conditions are favorable to the activity of the chromatophores growth will be greater than where its contents are aggregated in the manufacturing centre—a supposition which is no more unreasonable than that which supposes that functional activity favors growth—then in the region of shadow new chromatophores are formed, either by budding from or in relation to an existing centre. These in turn give rise to new centres in a like manner. The bar of shadow is now reflected on the surface of the animal by a bar formed of chromatophore branches. Hippolyte has grown into its surroundings."

"Further, if we accept a recent explanation of absorption color photography, we can see how the color of this bar of shadow comes to resemble that of the object that casts it. For Wiener has shown (1895) that a combination of substances may exist so sensitive to light as to be decomposed thereby, and give rise to a pigment of the same color as that of the incident light. If we postulate such a substance or combination in the chromatophores of Hippolyte, then the bar which we have just seen produced will be of the same color as that of the object which throws the shadow. We may then picture the mode whereby *Hippolyte varians* becomes infinite in variety."

[1] *Phil. Trans. Roy. Soc.*, London, Vol. 196, 1904, pp. 327–8.

We may suppose that by somewhat the same process the shadows cast on the bodies of primitive tigers, antelopes, reptiles, birds, fishes, caterpillars, etc., produced stripes, bars and spots. I think that these observations, coupled with the experiments of Steinach and those of Poulton on the formation of pigment in the pupæ of butterflies, will enable us to understand how the markings of animals arose. Keeble and Gamble add that the results obtained with respect to background as the chief factor in inducing pigment movement in Crustacea offer a curious and interesting parallel to the results of Prof. Poulton, though for his word "formation" they would substitute that of "movement." With this change the outcome of Poulton's experiments "summarizes the state of affairs in Crustacea."

23. Conclusions.

1. The alleged cases of Müllerian mimicry can be explained by convergence due to the action of similar physical and climatic causes. The attacks of birds are a negligible factor.

2. The oftentimes striking and wonderful resemblances in coloration and markings are the result of pigmentation caused by exposure to the combined effects of sunlight and shade, and due—

a. To the repetition of the fundamental colors, brown, black, red, yellow, in insects of different orders, as well as animals of different classes, living exposed to direct sunlight, and often having exceptional diurnal or light-loving habits in contrast with the lucifugous habits of the other species of the genus, family or order.

b. The similarity of design appears in many, if not most, cases to be due to the repetition of markings with identical shapes or patterns, *i.e.*, lines, bars, which are eventually broken up into spots and repeated *ad infinitum*, owing to the economy everywhere seen in Nature of material and design, differing in details in different groups, owing to their different origin and hereditary constitution.

It is no wonder therefore that there should be apparent cases of mimicry in regions like the hot and humid forest-covered plains of Brazil and the East Indies, or the upland hot plains of southern Africa, or in Australia where there are yellow flies, beetles and Hymenoptera with a broad black band around the abdomen, hence curiously mimicking each other.

3. Extreme advocates of Batesian and Müllerian mimicry appear to entirely overlook the operation of the physical agents of sunlight

or excessive contrasts of light and shade combined, moisture and dryness, differences in environment or other climatic causes as affecting the amount and distribution of pigment. These markings probably gradually arose simultaneously in a given region in all the individuals, and not as a variation in a single individual, which is supposed to have became favored in the struggle for existence.

4. While the initial causes therefore are Lamarckian, natural selection as a preservative process may form a subordinate factor.

5. To claim that Müllerian mimicry is due to the attacks of birds, is to overlook the fact of the existence of stripes, bars and spots on the wings of paleozoic insects which flourished before the appearance of birds, and even of modern types of lizards.

6. As observers and collectors differ so greatly in their interpretation of the facts, the subject of protective mimicry, even if the data and arguments here presented do not to some seem conclusive, should at least be considered as an open one, the importance of Bates and of Müller's hypotheses as factors in evolution having been in some quarters unduly magnified.

We hope that no one will suppose that there is any disposition on our part to underestimate the value of the labors of either Bates or Fritz Müller. On the contrary, no one has a higher appreciation of their work than myself. Mr. Bates' essay shows that he should rank with Darwin and Wallace; while Fritz Müller's brief article were in the nature of suggestions confined to a few pages. As a zoologist he ranks with Darwin in fertility of suggestion and as an original co-founder of evolution. Darwin's own estimate of Müller's little paper is given in *More Letters of Charles Darwin*, wherein he says that Müller's views on mimicry are "too speculative to be introduced into my book" (p. 91).

Stated Meeting, December 16, 1904.

President SMITH in the Chair.

Mr. Alden Sampson read a paper entitled "A Deer's Bill of Fare."

Dr. M. J. Greenman, on behalf of Henry W. Fowler, presented a paper entitled "Description and Figure of *Coregonus nelsonii* Bean."

The President delivered his Annual Address which included "A Chapter in Electro-Analysis."

DESCRIPTION AND FIGURE OF COREGONUS NELSONII BEAN.

(Plates VIII and IX.)

BY HENRY W. FOWLER.

(*Read December 16, 1904.*)

Through the courtesy of Drs. Horace Jayne and M. J. Greenman I have recently had the opportunity of examining several large examples of the above White Fish received at the Wistar Institute of Anatomy in Philadelphia. As this species is only known from Dr. Bean's description and several references, it is of value to have more detailed information for the comparison of the species.

COREGONUS NELSONII Bean.

Proc. U. S. Nat. Mus., VII, 1884 (1885), p. 48. Nulato, Alaska. (E. W. Nelson.)

Head 5; depth 4; D. III, 11; A. III, 9; P. II, 16; V. I, 10; scales 81 in lateral line to base of caudal; 11 scales between origin of dorsal and lateral line, and 9 between latter and origin of ventral; about 33 scales before dorsal; width of head $1\frac{7}{8}$ in its length; depth of head $1\frac{1}{5}$; snout 4; eye $7\frac{1}{2}$; maxillary $4\frac{1}{8}$; interorbital space $3\frac{1}{10}$; mandible $3\frac{1}{4}$; second dorsal ray $1\frac{1}{4}$; first anal ray $1\frac{3}{5}$; length of pectoral $1\frac{1}{3}$; ventral $1\frac{1}{3}$; least depth of caudal peduncle $2\frac{1}{8}$.

Body elongate, oblong, robust, compressed, sides flattened, back hardly elevated, and profiles similar though upper is a little more convex or gibbous anteriorly than lower. Greatest depth about origin of ventral. Caudal peduncle stout, compressed, and its least depth about equal to its length.

Head small, compressed, sides flattened, and upper profile a little concave. Snout convex, a little produced and broad. Eye small, circular, and placed near first third in length of head. Mouth inferior, small, gape a little curved in profile, and its width much greater than gape. Lips rather thick or fleshy. No teeth either in jaws, on roof of mouth or on tongue. Tongue not free. Nostrils adjoining, a little nearer front of eye than tip of snout, and anterior with a fleshy or cutaneous rim, posterior margin enlarged a little and more or less conceals posterior nostril. Interorbital space convex, elevated more medianly. Opercles with striæ. Opercular flaps rather broad.

Gill-opening large, extending forward a little over half way in length of head but not to posterior margin of eye. Rakers 6 + 14, short, pointed, about $3\frac{1}{2}$ in longest filaments. Filaments long, longest 5 in head. No pseudobranchiæ. Branchiostegals 8, rather large and conspicuous, and graduated to uppermost which is largest. Isthmus rather long, triangular and with convex surface.

Scales small, cycloid, well exposed and more or less of equal size except on base of caudal and on breast. None on chest. Distributed in longitudinal even series. A pointed scaly flap in axil of ventral. Head and fins naked, except base of caudal. Lateral line continuous, more or less parallel with lower profile most of its course and extending posteriorly along middle of side of caudal peduncle to base of caudal. Tubes simple.

Origin of dorsal nearer that of adipose fin than tip of snout or a little behind tip of pectoral, high, and second branched ray longest. Adipose fin well developed, beginning a little behind that of anal, and length of fin a trifle less than half length of head. Height of adipose fin nearly half of its base. Anal originating much nearer base of caudal than origin of ventral, lower than dorsal, and first branched ray highest. Caudal robust, deeply emarginate, and lobes pointed. Pectoral rather long, about equal to height of dorsal, and reaching a little over half way to ventral. Ventral inserted behind origin of dorsal, a little longer than first branched anal ray, and reaching half way to origin of anal. Vent close in front of anal.

Color in alcohol more or less faded uniform brown, lower side and under surface paler. Fins brownish and immaculate. Each longitudinal series of scales on trunk with median portion paler so that body has appearance of many alternate dark and light longitudinal bands, most distinct or pronounced above. Iris slaty.

Length about 24 inches.

No. 7258, Wistar Inst. Anat. Phila. Meade River, Alaska. Nov. 1897. E. L. MacIlhenny. This is an adult female. Also three others which show the following: Head 5 to $5\frac{1}{8}$; depth $3\frac{5}{8}$ to $4\frac{1}{3}$; D. III, 10 or III, 11; A. III, 9 or III, 11; scales 80 or 81 in lateral line to base of caudal and 4 to 6 more continued out on latter; gill-rakers about 12 on lower half of first arch and 7 to 9 on upper half; total length 21 to 24 inches. The smallest was obtained at Point Barrow, Alaska.

The following notes relative to the alimentary canal are expli-

cable by means of Plate IX, and were made from a rough dissection of the example described above.

Pharynx rather capacious.

Stomach large, elongate, sack-like and somewhat muscular anteriorly.

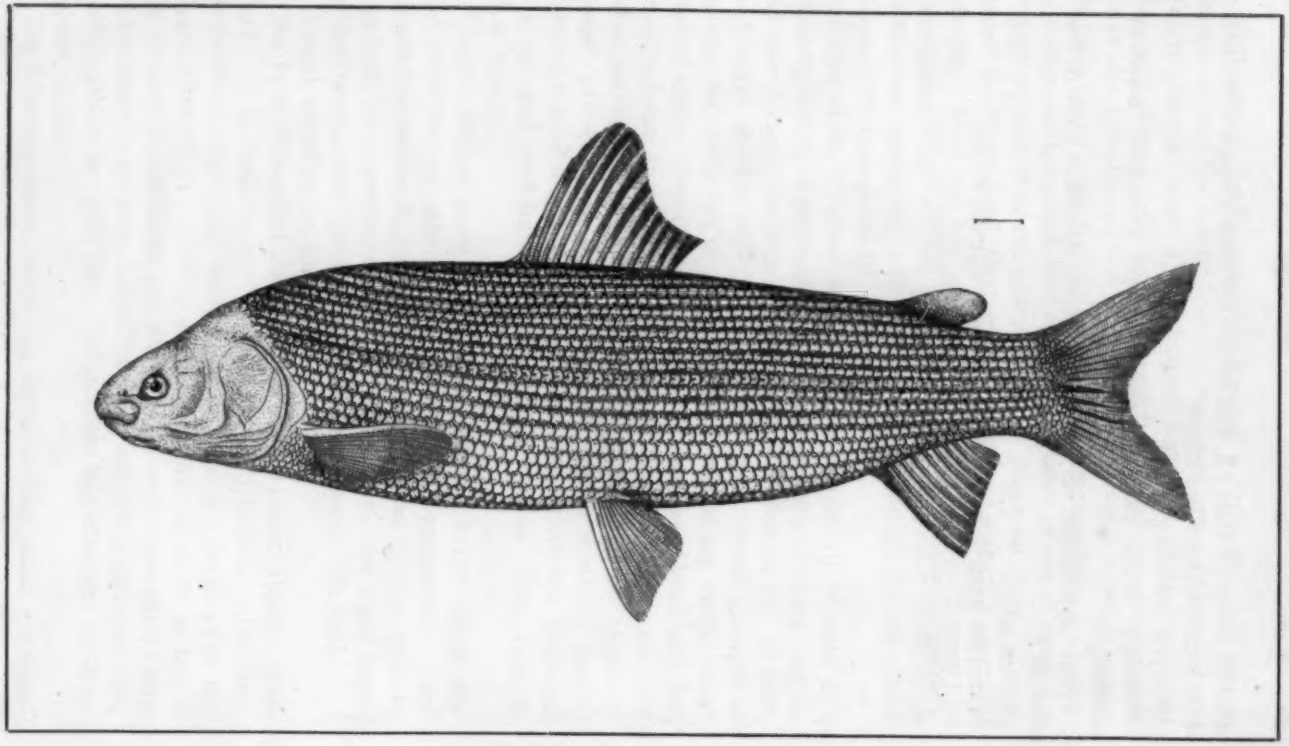
Pyloric appendages very numerous, rather short and more or less subequal.

Spleen large.

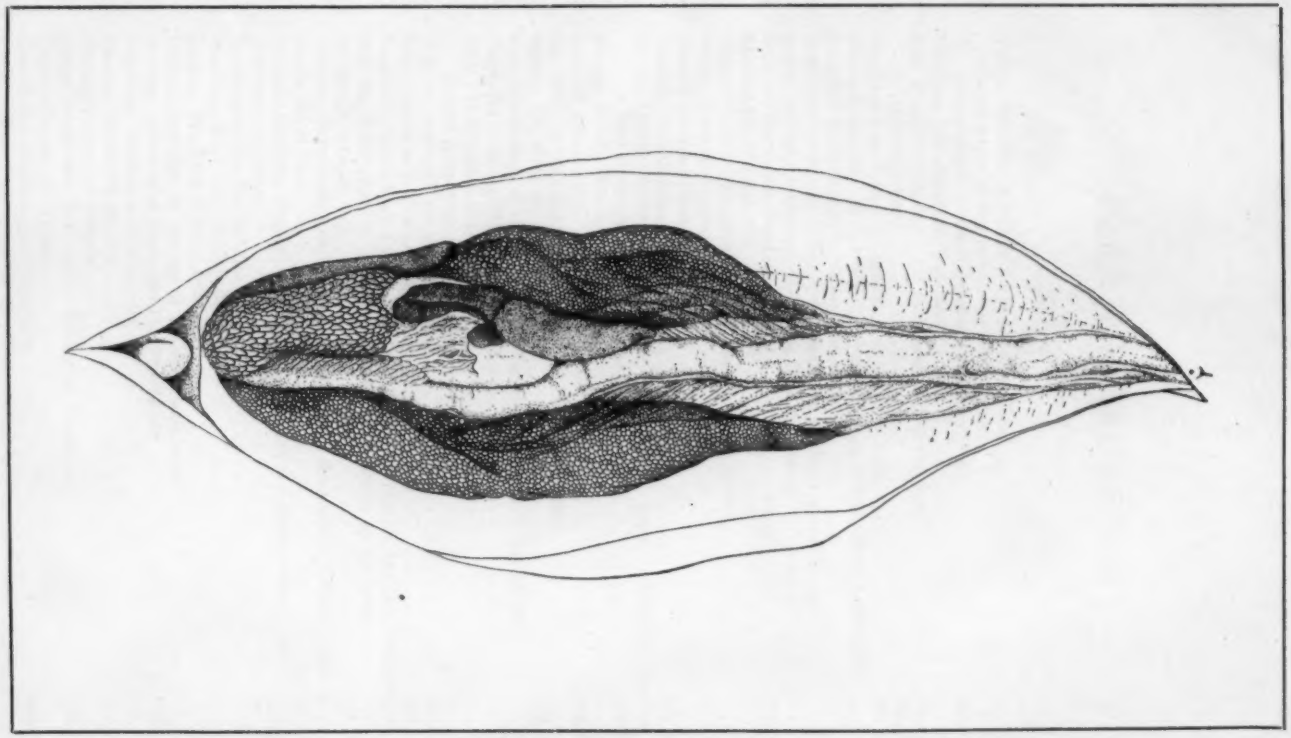
Intestine straight from pylorus, without sigmoid curve.

Philadelphia, Academy of Natural Sciences, December 15, 1904.

PROC. AMER. PHILOS. SOC. XLIII, 178, DD. PRINTED JAN. 23, 1905.



FOWLER—COREGONUS NELSONII BEAN.



FOWLER—COREGONUS NELSONII BEAN.

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